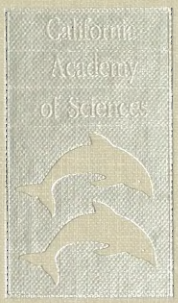
Proceedings of the 11th International Diatom Symposium

San Francisco, California
12–17 August 1990

Edited by

JOHN PATRICK KOCIOLEK



California Academy of Sciences
San Francisco, California

Proceedings of the 11th International Diatom Symposium

San Francisco, California

12 – 17 August 1990

Edited by John Patrick Kociolek

Diatom Collection, California Academy of Sciences

Published by the California Academy of Sciences

San Francisco, California

Memoirs of the California Academy of Sciences, Number 17

11
c17X
NH

SCIENTIFIC PUBLICATIONS COMMITTEE:

Thomas F. Daniel, *Editor-in-Chief*
Ann Senuta, *Managing Editor*
John Patrick Kociolek, *Volume Editor*
Katie Martin, *Editorial Assistant*
Robert C. Drewes
Wojciech J. Pulawski
Adam Schiff
Gary C. Williams

© 1994 by the California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

All rights reserved. No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage or retrieval system, without permission in writing from the publisher.

Library of Congress Catalog Card Number 94-070113
ISBN 0-940228-34-3

Proceedings of the 11th International Diatom Symposium

12 – 17 August 1990

SMITHSONIAN
MAR 25 1999
LIBRARIES

Table of Contents

Foreword 1

Announcements

Chandra, A. Excerpts from the will of the late (Mrs.) Savitri Sahni (1902–1985) 3

Morphology, Taxonomy, and Systematics

Crawford, R. M. Transmission electron microscopy and diatom research 5

Lee, J. J. Diatoms, or their chloroplasts, as endosymbiotic partners for Foraminifera 21

Rivera, P. S. and H. L. Barrales. *Asteromphalus sarcophagus* Wallich and other species of the genus off the coast of Chile 37

Loseva, E. Are both *Rhizolenia curvirostris* Jousé and *R. barboi* Brun found in Pleistocene sediments of northeastern Europe? 55

Ferrario, M. E. and E. A. Sar. Valve morphology of *Coscinodiscus janischii* Schmidt (Bacillariophyceae) 63

Gallagher, J. C. Genetic structure of microalgal populations. I. Problems associated with the use of strains as terminal taxa 69

McCartney, K., J. Ernissee, and D. E. Loper. Mathematical modeling of Silicoflagellate skeletal morphology and implications concerning skeletal latticeworks ... 87

Conley, D. J., P. V. Zimba, and E. Theriot. Silica content of freshwater and marine benthic diatoms 95

Makarova, I. V. The morphology of marine genera of the family Thalassiosiraceae Lebour emend Hasle 103

Moreno, L. and S. Licea. Morphology of three related *Coscinodiscus* Ehrenberg taxa from the southern Gulf of Mexico and coastal North Pacific of Mexico ... 113

Reichardt, E. Two new species of the genus *Surirella* from Lake Turkana, east Africa 129

Kilham, S. S. Do diatom "superspecies" ever evolve? 135

Fukushima, H., T. Ko-Bayashi, H. Ohtsuka, and S. Yoshitake. Morphological variability of *Navicula recens* (Lange-Bertalot) Lange-Bertalot 143

Czarnecki, D. B. The freshwater diatom culture collection at Loras College, Dubuque, Iowa 155

Compère, P. Diatoms from hypersaline inland waters of Egypt 175

John, J. *Mastogloia* species associated with active stromatolites in Shark Bay, west coast of Australia 189

Johansen, J. R., S. Lacognata, and J. P. Kociolek. Examination of type material of *Denticula rainierensis* Sovereign 211

Hargraves, P. E. and A. M. Schmid. Morphology, cytology, and growth characteristics of the diatom *Planktoniella sol* (Wall.) Schütt 221

Kociolek, J.P., L. Sicko-Goad, and E. F. Stoermer. Cytoplasmic fine structure of two *Encyonema* species 235

Williams, D. M. Ontogeny and phylogeny in the genus *Tetracyclus* 247

Khursevich, G. Evolution and phylogeny of some diatom genera of the class Centrophyceae 257

Khursevich, G. Morphology and taxonomy of some centric diatom species from the Miocene sediments of the Dzhilinda and Tunkin hollows 269

Kobayasi, H., S. Kobori, and S. Sunaga. Taxonomy and morphology of two forms of the *Nitzschia sinuata* complex 281

Ognjanova-Rumenova, N., D. Temniskova-Topalova, and M. Valeva. Ultrastructure of *Fragilaria* Lyngbye species (Bacillariophyta) from neogene sediments in Bulgaria 291

Temniskova-Topalova, D., N. Ognjanova-Rumenova, and M. Valeva. Nonmarine biostratigraphy of some genera of the class Centrophyceae from southern Bulgaria 301

Licea, S. *Thalassiosira* species from the Southern Gulf of Mexico 311

Solliday, J. D. Morphological variations in fossil diatoms from Mono Lake 337

Grönlund, T. Lagoonal diatom flora of the Holocene Baltic Litorina Sea in comparison with the Eemian Baltic sea flora 349

Marine Palaeoecology

Loseva, E. Marine Pleistocene diatom assemblages of northeastern Europe 359

Risberg, J. and P. Sandgren. Shore displacement in the Stockholm area, Sweden, during the early Holocene as recorded from diatom and magnetic analysis—A preliminary report 371

Williams, K. M. and S. L. Forman. Diatoms and sediment of a modern glacial fjord environment, western Spitsbergen 387

Fourtanier, E. and R. Oscarson. Ultrastructure of some interesting and stratigraphically significant diatom taxa from the Upper Palocene to Lower Eocene sediments of ODP site 752, eastern Indian Ocean 399

White, L. D. Diatom biostratigraphy of chert intervals in the Miocene Monterey formation at Pt. Reyes, Pt. Año Nuevo, Mussel Rock, and Lions Head, California 411

Brackish and Marine Ecology

Leskinen, E. and G. Hällfors. Dynamics of epiphytic diatoms on *Cladophora glomerata* in the Tvärminne Archipelago, northern Baltic Sea 425

Fryxell, G. A. Planktonic marine diatom winter stages: Antarctic alternatives to resting spores 437

Marshall, H. Spatial and temporal diatom relationships in the lower James River, Virginia, U. S. A. 449

Freshwater Palaeoecology

Aasheim, S. Diatom stratigraphy and environmental history of a small lake basin in southwest Norway. 1. The last 4000 years 459

Main, S. P. Diatoms in alkaline peat: Preservation and extraction 465

Kovári-Gulyás, E. Well-preserved diatoms in limnic opals of Hungary 473

Harper, M. A. Did Europeans introduce *Asterionella formosa* Hassall to New Zealand? 479

Krebs, W. N. The biochronology of freshwater planktonic diatom communities in western North America 485

Metcalfe, S. and P. Hales. Holocene diatoms from a Mexican crater lake—La Piscina de Yuriria 501

Wasell, A. Diatom-stratigraphy in the sediment of "Skua Lake," Horseshoe Island, Antarctica. Preliminary report 517

Whitmore, T., M. Brenner, and X. L. Song. Environmental implications of the late Quaternary diatom history from Xingyun Hu, Yunnan Province, China 525

Anderson, N. J. Inferring diatom palaeoproduction and lake trophic status from fossil diatom assemblages 539

Shero, B. R. Diatom assemblages of the past 11,000 years from the Yellowstone Lake basin, Wyoming, U. S. A. 549

Freshwater Ecology

Rogers, C. E. and L. Sicko-Goad. Effects of chemical fixation on flow cytometric properties of diatoms 557

Watanabe, T. and K. Asai. Numerical estimation of organic pollution based on the attached diatom assemblage in Lake Biwa and its inflows 567

Kiss, K.T. and G. Pajak. Seasonal change of diatoms in the plankton of the Vistula River, above and below the Goczalkowice Reservoir, Poland 583

Burton, T. M., M. P. Oemke, and J. M. Molloy. Effects of grazing by the Trichopteran, *Glossoma nigrior*, on diatom community composition in the Ford River, Michigan 599

Burton, T. M., M. P. Oemke, and J. M. Molloy. Effects of stream order and alkalinity on the composition of diatom communities in two northern Michigan river systems 609

Carney, H. J., D. A. Hunter, and C. R. Goldman. Seasonal, interannual and long-term dynamics of planktonic diatoms in oligotrophic Lake Tahoe 621

Gell, P. A. and F. Gasse. Relationships between salinity and diatom flora from some Australian saline lakes 631

Huttunen, P. and J. Turkia. Diatoms as indicators of alkalinity and TOC in lakes: Estimation of optima and tolerances by weighted averaging 649

Katoh, K. Spatial variation of diatom assemblages in Minami-Aizu moors, Fukushima Prefecture, Japan: The effect of pool size 659

Yoshitake, S. and H. Fukushima. Estimation of recovery of water quality in urban water system by diatom flora 665

Foreword

The 11th International Diatom Symposium was held 12–17 August 1990, in San Francisco, on the campus of San Francisco State University, and it was sponsored in part by the California Academy of Sciences. The meeting was officially convened by Dr. John Barron with the support of the Bay Area Diatomists Group. The Local Organizing Committee, composed of Dr. Barron, Al Mahood, Margaret Hanna, Dr. Elisabeth Fourtanier, Dr. Lisa White, Dr. Eileen Hemphill-Haley, Ray Wong, and James Fidiam, provided organizational, logistical and other practical support, and without them the meeting would not have been as smooth as it was. The committee insisted the main goal of the San Francisco meeting was to make the meeting truly an international one. This original intent was realized as over 200 diatomists from over 30 countries participated in the meeting.

It was my hope in producing this *Proceedings* volume that the diversity seen in the attendance of the San Francisco meeting would be mirrored by the submissions to the volume. This goal has been realized in part as evidenced by the large number of submissions and the diversity of contributors. There is also diversity in the wide range of taxonomic groups studied, and a diversity of habitats, including fossil and Recent in both the freshwater and marine environments. The wide range of subjects, localities and contributors suggests to me that, like the goal for the meeting, the intent to make this *Proceedings* reflect the international spirit and flavor of the San Francisco meeting has been attained.

I would like to acknowledge the leadership, encouragement and friendship of John Barron, for without his enthusiasm and hard work the meeting would never have happened. Special thanks are due to all the members of the Local Organizing Committee for their diligence, planning and enthusiasm for the meeting. Members of the Department of Invertebrate Zoology and Geology of the California Academy of Sciences helped in many ways to make the meeting a success; the efforts of Mary Alice Tatarian and Patricia Dal Porto require special recognition. The reviewers of the contributors provided excellent and especially prompt peer review. The patience and good humor of the contributors throughout what has probably seemed an eternity before their scientific efforts see publication are particularly appreciated. Finally, Ann Senuta, managing editor of the Scientific Publications Department of the California Academy of Sciences, has shown great skill and patience in taking my edited/revised copy and producing this high-quality volume. I am indebted to her for all of her hard work.

J. Patrick Kociolek

Excerpts from the Will of the Late (Mrs.) Savitri Sahni (1902–1985)

by

Anil Chandra

Birbal Sahni Institute of Palaeobotany, Lucknow 226007, India

> "It is my desire that in token of my love and devotion to that fine and great spirit of my noble husband late Professor Birbal Sahni and in the pride of my illustrious husband's unique lofty ideals, a portion of my ashes be strewn in the flower beds around his 'Samadhi' at the Birbal Sahni Institute of Palaeobotany, Lucknow.
>
> "To my palaeobotanist colleagues the world over whom I hold in very high regard and affection, I offer my deep gratitude for their cooperation in the cause of science and towards fulfillment of our ideal, which has been a source of great encouragement to me. I express for them my unbounding affection and my all blessings follow them ever. I realize what great it is in life to have been given the great gift of receiving such unstinted affection from all over the palaeobotanical world, and I am beholden to them."

With such noble feelings, the late Padamsri (Mrs.) Savitri Sahni founded Birbal-Savitri Sahni Foundation with the following programs:

(1) International Research Collaborative Programmes for exchange of scientists between the Birbal Sahni Institute of Palaeobotany, Lucknow, and palaeobotanical organizations abroad; this would be known as the Birbal-Savitri Sahni Collaborative Research Programme.

(2) Birbal-Savitri International Fellowships would be awarded to young palaeobotanists/earth scientists for carrying out research in any specialized branch of palaeobotany in India.

(3) Birbal-Savitri Sahni International Awards would be given in alternative years to an outstanding scientist excelling in palaeobotanical and allied fields; awards would carry a cash prize of 25,000 rupees and a plaque in gold and silver. Nominations for such award may be forwarded to the Foundation between April 10th and April 26th every year.

(4) Savitri Sahni Samman, founded by friends and admirers of Mrs. Savitri Sahni for her dedication to the cause of palaeobotany, would carry a cash prize of 10,000 rupees, including a medal that is to be given annually on January 22nd to a palaeobotanist for outstanding research work.

(5) Savitri Sahni Smarak Lecture, instituted with cost donations from well-wishers of Mrs. Savitri Sahni, carries a token honorarium of 5,000 rupees for an invited lecture every

year on September 19th in any specialized field of palaeobotany. The lecture would be published as a monograph under the auspices of the Birbal-Savitri Sahni Foundation. These programs are meant to promote palaeobotanical and allied sciences the world over, for which Mrs. Savitri Sahni donated every bit of her belongings to the nation and entrusted to Birbal-Savitri Sahni Foundation. The entire residence of the Sahni's, situated at the banks of the river Gomti, is planned to be converted into a museum-cum-guest house, and a "palaeogarden" is also being planned to develop at the site where her last remains were consigned to flames.

For further details one may contact: Dr. Shyam C. Srivastava, Secretary, Birbal-Savitri Sahni Foundation, 686 Birbal Sahni Marg, Post Bag No. 1, New Hyderabad Post Office, Lucknow 226 007, India.

Transmission Electron Microscopy and Diatom Research

by

Richard M. Crawford

Alfred-Wegener-Institut für Polar und Meeresforschung,
Postfach 120161, Columbusstrasse, D-2850 Bremerhaven, Germany

with 2 plates

Abstract: Many of the most important questions concerning diatom structure and biology have been answered using transmission electron microscopy. Some of the major advances are reviewed here. Unresolved problems are identified, and new questions are raised with a plea for a more balanced approach to the microscopy of diatoms.

Introduction

Throughout its history, diatom microscopy has been somewhat restricted in its field of interest. For the first 150 years, light microscopists concentrated on the morphology of the major components of the frustule—the valves—and neglected the ''minor'' components of the cingulum and the soft parts of the cells such as the nuclei and plastids. In the subsequent 45 years or more, electron microscopists have covered much the same ground, albeit in greater detail and with the same general purpose, i.e., to arrive at a classification that received common agreement and reflected as closely as possible the natural phylogeny of the group.

Furthermore, most published papers included information from scanning electron microscopy (SEM) and relatively little from transmission electron microscopy (TEM). This is regrettable. Just as valuable information from light microscopy has been seriously overlooked (Cox 1981) so too has the abundance of morphological markers within the diatoms by all but a few workers. Such markers—manifestations of an explosive radiation of evolution—have been the source of important information on morphogenesis as they appear in strict sequence following the events of cytokinesis under the control of the nucleus.

The early electron microscopy of diatoms was, in fact, performed using TEM, and the first pore plates were seen in the remarkably high-quality micrographs of direct preparations by Kolbe and Golz (1943). Hustedt (1945) followed, and then Desikachary (e.g., 1954), Helmcke and Krieger (1953–1977) and, during most of the 1950s, Okuno (see Okuno 1962 for a list of many of his works). Most of these studies used direct preparations, and sections were not obtained until the early 1960s.

These early pioneers would have had some concept of the wealth of information awaiting discovery but little idea that TEM studies would be overtaken, at least in terms of usage, by SEM. Paradoxically, the leap in potential resolution may have been too great for the peace of mind of many light microscopists (see, for example, the misgivings of Hendey 1959). Certainly the preparative techniques of SEM proved much simpler for the majority of us as we continued to collect comparative morphological data with the SEM.

Rather than tackle the formidable task of assessing the progress made in electron microscopy as a whole, I will briefly focus on the considerable achievements of a small number of workers who have turned to some neglected questions, largely with TEM, and then I will attempt to establish what problems remain to be addressed.

(1) How is the cell wall morphology faithfully reproduced in successive generations?

This question is complex, and a number of different aspects are best considered separately.

The Role of the Nucleus and Associated Structures in Cell Division and New Wall Formation

Nuclear division precedes cell division and, as we know from light microscopy, is a prerequisite of half-frustule (valve + hypocingulum) formation. Indeed, nuclear migration occurs in many genera, and even though cell wall formation can begin before the nuclei are in position, the nucleus is generally found close to the developing valve. Few comprehensive series of sections have been made, and fixations have often been poor, but several of the features associated with the nucleus seem to be directly involved in wall morphogenesis.

Some of the structures associated with the nucleus were observed in the classical light microscope studies on *Surirella* by Lauterborn as early as 1896, and this work has been beautifully corroborated by Pickett-Heaps et al. (1984) using TEM. Other studies using the TEM include those of Manton et al. (1969a, b; 1970a, b) on mitosis and meiosis in *Lithodesmium*; Drum and Pankratz (1964), again on *Surirella*; and Crawford (1973) on *Melosira*. More recently, detailed studies of mitosis and wall morphogenesis in a number of genera by Pickett-Heaps and co-workers have provided a much clearer picture for diatoms and perhaps a better understanding of the behavior of the mitotic spindle in general (Pickett-Heaps 1987; Pickett-Heaps et al. 1991). Furthermore, the structure and behavior of the spindle, microtubule center, and polar complex promises valuable phylogenetic information (e.g., Pickett-Heaps 1983) even if only some of these structures are involved in cell division and successive events. Nuclear migration is affected by microtubules under the control of the microtubule center (MC), which disappears at metaphase only to reappear later in mitosis. Its role in valve morphogenesis of centric diatoms is "less easy to estimate" (Pickett-Heaps et al. 1991), and Schnepf et al. (1980) demonstrated little effect of microtubule inhibitors on the formation of *Attheya* frustules. Schmid (1980) and Blank and Sullivan (1983) have shown that the distribution of tube processes in some centrics and the development of the raphe in some pennates is upset but the general wall morphology is not. Nevertheless, the MC is closely involved with the SDV in pennate diatoms, for example, *Nitzschia*, *Hantzschia*, and *Pinnularia*. In the former two the MC moves with the SDV towards an off-center position or to the developing raphe. However, the MC is not concerned with movement of the SDV, because in *Achnanthes* the MC and subsequently the SDV moves away from the site of raphe development and the raphe slit is filled in (Boyle et al. 1984) The silica deposition vesicle itself is always present and is the focus of events throughout silica wall formation.

The functions of the microtubules also appear to differ. They are intimately associated with the developing raphe in pennates, more so in some genera than in others (Pickett-Heaps et al. 1991) and with developing setae in some centrics. The raphe fibre is another feature closely involved in controlling wall morphogenesis, although it is unclear whether it is done so to shape the valve as, for example, in *Pinnularia* (Pickett-Heaps et al. 1979), or to prevent silica deposition (Edgar and Pickett-Heaps 1984), or both (Pickett-Heaps et al. 1991).

Similar material to the raphe fibre has been found beneath developing rimoportulae of one species each of *Ditylum*, *Chaetoceros*, and *Stephanopyxis* and two species of *Odontella* by Li and Volcani (1984, 1985a, b, c,). Crawford and Schmid (1986) have proposed that such material may, in general, prevent silica deposition wherever it occurs. Pickett-Heaps et al. (1991) echo this proposal and illustrate similar granular material within the SDV and the lengthening hollow tube of the rimoportule in *Ditylum* as well as granular material subtending the fultoportule.

This area of research would surely repay further study with improved fixation techniques. Perhaps, for example, freeze substitution may show this material to be more widespread than we know at present. Both the labiate process (rimoportule) apparatus (LPA) of the centrics and the raphe fibre disappear on completion of that part of the valve. Li and Volcani (1985b) proposed that the rimoportule region is the primary silicification site for valve formation in centric diatoms. Crawford and Schmid (1986) objected to this proposal on the grounds of Li and Volcani's (1985c) interpretation of events during morphogenesis of *Odontella sinensis*, but there are other reasons for caution. These include the large number of rimoportulae in the valves of some genera, for example, *Podosira*, *Stictocyclus*, and *Coscinodiscus* ; the complete lack of tube processes of any kind in some genera, for example, *Chrysanthemodiscus*, and the lack of a counterpart for the rimoportula as a focal point for the development of elements of the cingulum. As Pickett-Heaps et al. (1991) point out, the relationships of the rimoportule to some pattern centers or annuli (von Stosch 1977) as in *Ditylum* is coincidental.

The existence of a cytoskeleton that breaks down during meiosis and oogamy and reconstitutes after the auxospore of *Thalassiosira eccentrica* reaches maturity has been investigated by Schmid (1984a), and from reports of the many processes mentioned above it is clear that such an organisation is complex among diatoms. Further examination throughout the group is warranted.

The Role of Cytoplasmic Vesicles, Membranes, etc., in New Wall Formation

The silica deposition vesicle (SDV) was discovered by Reimann and by Drum and Pankratz in 1964, and its membrane was given the name "silicalemma" in 1966 (Reimann et al. 1966). Stoermer et al. (1965) demonstrated close involvement of the SDV with the developing cell wall. Also appearing at this time was the series of micrographs of thin sections by Drum et al. (1966), which still repay examination. All of these observations eventually paved the way for the work of Dawson (1973) and Chiappino and Volcani (1977) on pennate diatoms and Schnepf et al. (1980) and Schmid on centrics (1984a, b 1985a, b). There have also been numerous recent contributions by Pickett-Heaps and co-workers that referred to the above.

Before, or just after, completion of cytokinesis a SDV appears beneath the plasmalemma of each daughter cell. Derived by the fusion of small vesicles (Schmid and Schulz 1979), which are presumed to be dictyosome derived, the vesicle expands centrifugally. In the pennates, this expansion is essentially horizontal (Chiappino and Volcani 1977; Pickett-

Heaps 1983), but development is asymmetric and manifest, for example, in Voigt discontinuities (Mann 1983). In the centric *Coscinodiscus wailesii*, Schmid (1986a, b) showed a complex horizontal development of threads of the SDV that circumscribe the areola before expanding vertically and then again horizontally to close off the loculae or chambers in the developing valve. By very careful control of the osmotic potential of the fixative, Schmid demonstrated the involvement of a number of types of vesicles and even the mitochondria, dictyosomes, and cytoskeletal elements in moulding the valve shape and the areolae size. Schmid (1984b) also proposed control on a finer scale by vesicles from the dictyosome that lie directly beneath the pore plates, but she also pointed out that the SDV does not have a moulding capacity, thereby encouraging us to consider two separate concepts here—namely, the silica deposition itself and the moulding of the structure.

Since the communication of the present paper, Pickett-Heaps et al. (1991) have published their review of valve formation in which they distinguish between "membrane-mediated morphogenesis" and "macro-morphogenesis." The former is brought about within the SDV. More careful studies like those of Schmid's are needed before we can confidently explain the moulding and pattern reproduction. The more complex frustules of centric diatoms are likely to be more rewarding here, but the enigmatic question "How does the diatom reproduce its discrete pattern?" may prove elusive for some time. Part of the answer, of course, may come from investigation of the third aspect.

The Deposition of the Silica and its Control

Even among those workers sectioning diatoms, few have examined the developing siliceous component at high magnification. Borowitzka and Volcani (1978) and Schmid and Schulz (1979) were the first to show that silica is added in the form of particles, but there is still uncertainty regarding the establishment of the fundamental pattern of the valve (Pickett-Heaps et al. 1991). Polysaccharides and proteins have been separately proposed for a template for the pattern.

Somewhat later in the process there appears to be variation in the way the valve is built up. For example, Li and Volcani (1984, 1985a) reported a change in *Ditylum brightwellii* from a smooth basal layer through microfibrillar addition to one of hexagonal columns. On the inside surface however, hexagonal columns are absent. In *Odontella* species, only the basal layer and microfibrillar form is found. In most of the centric diatoms (*Ditylum* may be an exception here; see Li and Volcani 1984, Figs. 11a, b) addition of the silica occurred on the biological outside of the wall component in direct contrast to the situation in *Amphipleura pellucida* (Stoermer et al. 1965), in *Navicula cuspidata* (Edgar and Pickett-Heaps 1984), and in *Pinnularia* (Pickett-Heaps et al. 1979). There the silica is added on both sides of a kind of middle lamella. In *Odontella* (Crawford and Schmid 1986) and *Striatella* (Roth and De Francisco 1977), development appears to be only towards the biological inside of the valve, but more species need to be investigated before any firm statements are made. Just as importantly, the araphid group must also be examined.

In all developing valves examined to date, completion is recognized by the smooth appearance of the silica on all surfaces. This leads one to ask three further questions. How is the process started? How is the deposition controlled? And how is completion achieved? The first question is likely to be the easiest to answer insofar as the process will ultimately have been triggered by nuclear division leading to the production of the SDV and the supply of Si and other wall components. The deposition itself may either be controlled by the time for which the process is allowed to continue, or by means of its rate (Pickett-Heaps et al. 1979). Intuitively, one would argue that the simpler would be through

maintaining a constant rate of deposition that was allowed to continue longer in thicker parts of the frustule. Control of the rate is likely to be through the organic template or matrix, which is considered by several workers to exist in the SDV (e.g., Nakajima and Volcani 1969), but Lee and Li suggest (pers. comm.) that the rate is controlled by the supply of membrane, which is itself determined by the production of glycoproteins.

Concerning the third question; clearly part of the answer is through genetic signals passed through the membrane system. Schmid has observed a switch in dictyosome production from silica transport vesicles to dark vesicles that she maintains may provide organic material to prevent further deposition. There are several reports from diatoms and other silica metabolising plants and animals that this organic material provides protection against dissolution. However, since the face of the siliceous element is rough during development (see above), a smoothing of the silica has to occur before this organic "sealing" process takes place in order to achieve the completely even surface found in many electron micrographs. Compare, for example, Li and Volcani's Figures 66 and 75 of *Ditylum* (Li and Volcani 1985a). It appears most likely that the smoothing of the frustule is brought about by control of the final stages of silicification *before* the switch of vesicle production, and it is the answer to how this is achieved that may prove the most elusive. It is difficult to imagine how a change from one vesicle type to another can bring all of the silica up to the same level before silicification ends.

The Fate of the Membranes Involved in Cell Wall Formation

This final step in wall morphogenesis has received attention from a number of workers (see references in Schulz 1984), but it was Schmid (1986a, b) who investigated this problem in depth and presented four possible models for the fate of these membranes. One of these (M3) seems unlikely (Schmid 1986a) as it proposes de novo synthesis of plasmalemma in the "new" half of the cell. Nevertheless, this strategy was favored by Schulz (1984). Two other models (M1, M2) involve fusion at the valve edge of the inner profile of the SDV in the "new" half of the cell with the plasmalemma in the "old" half. One of these models sees the outer profile of membrane, SDV, and plasmalemma lost; the other sees them incorporated as organic matrix into the valve. The fourth model, (M4, and that favored by Schmid), envisages reticular fusion of SDV and plasmalemma at the center outside of the valve. Some membrane is lost to the outside, but retraction occurs at the valve edge and some of the membrane on the outside during maturation of the valve (plasmalemma and distal silicalemma) is internalized. At the same time, the incorporation of dense vesicles to the proximal silicalemma causes it to become plasmalemma-like. Schmid (1986b) calculates the area of membrane saved by this method and addresses the problems of timing of valve release and incorporation of organic matter into the frustule. It seems inconceivable to the author that much variation would exist in this fundamental process throughout the diatoms, but more work is called for to establish that this so.

(2) What is the function of the different cell wall components?

This question has seldom been asked, if at all, by light microscopists and only indirectly by electron microscopists. As the organelles such as rimoportulae, fultoportulae, ocelli, pseudocelli, rays, conopea, and partecta have been described, so possible functions have been proposed for them. However, we are still a long way from a complete explanation, and much needs to be done here, but I wish to confine my remarks to the two major wall components: the girdle bands and the valves.

The bands of the cingulum have been relatively neglected compared to the valves, but their function can be considered in the light of proposals that they, like the valves themselves, originated from siliceous scales (Round and Crawford 1981). The more obvious functions are, firstly, to ensure protection for the developing protoplast as the two parent valves pull apart from each other prior to cytokinesis and, secondly, to allow penetration of the sperm in oogamous species (Drebes 1977). The third possible function is to provide the means by which the dimensions of the cells can be controlled through variation of the number of components in the cingulum. This has obvious significance in the planktonic situation and has parallels in the control of filament length through alteration of the separation valve index in *Aulacoseira granulata* (Davey and Crawford 1986). Clearly, the greater the proportion of the frustule that the cingulum assumes, the more important it will be that the structure of the areolae resemble those of the valves. It is notable that in some genera where the cingulum is a relatively major component, similar vela have been shown by them. Good examples may be found in the Rhizosoleniaceae (Sundstrom 1986) in *Eucampia* and in *Acanthoceras* (Round et al. 1990). However, there are other genera where this is not obviously the case, for example, *Ditylum* and *Dactyliosolen* (Round et al. 1990).

As I have indicated above, we have come to regard the valves as the important part of the frustule simply because they are generally the largest. They may be the largest simply because they are polar (see Round and Crawford 1981; Mann and Marchant 1989 for evolutionary considerations), but perhaps we should pay greater attention to the cingulum and take account of its role in diatom biology.

That the valve itself provides a robust envelope that presumably deters at least some grazing predators while permitting light to penetrate to the plastids is usually taken for granted as is the fortuitous fact of nature for transmission electron microscopists that silica is opaque to electrons while being transparent to light. A function that has been investigated by a number of authors (Ross et al. 1977; Crawford 1979; Fryxell and Medlin 1981) is the provision of linking mechanisms on the outside of the valves in those species that do not exist as unicells, but this has been investigated more through SEM studies. The work of Schmid concerning the inner surface is an exception. Using a number of techniques, she has proposed that the inner apertures of the fultoportulae act as anchorage points for the cytoskeletal system (Schmid 1984a).

Prior to the publication of the first TEM micrographs of pore plates, most concepts of the areolae saw them as more or less simple holes in the frustule. We now know that there are indeed such holes in some genera, for example, *Fragilaria* (Crawford et al. 1985), *Corethron* (Crawford and Round 1989), and occasional simple pores scattered among the areolae in a number of other genera, for example, *Eucampia* (Round et al. 1990). True vela are, however, chiefly covered by plates of silica, the cribra, which may themselves have tiny pores or may only have areas of extremely weak silicification as Schmid and Schultz (1979) point out for *Thalassiosira*. Our investigations of a number of diatoms suggest the situation may be more complex.

Thin sections through the valve of the marine centric *Actinocyclus subtilis* (Andersen et al. 1986) have revealed an elaborate loculate valve with very fine pores on the outside surface that open inwardly, eventually, to a large chamber. This chamber is closed on the inner surface by fine siliceous projections that are supported by organic material as shown by sections treated with dilute hydrogen fluoride, which dissolves silica but leaves organic matter intact. A similar component was illustrated by Drum et al. (1966) in *Aulacoseira (Melosira) granulata*, and is shown here to be siliceous by hydrogen fluoride treatment. (Figs. 1–6). Interestingly, the organic layer extends under the whole of the mantle surface,

and siliceous projections extend upwards generally rather than to individual areolae. This component has also been found in the related species *Aulacoseira ambigua*, but what is interesting about both genera is that this organic/siliceous complex only occurs beneath porous areas of the valve (between arrowheads in Fig. 3), that is, beneath each areola in *Actinocyclus* but beneath the entire valve mantle in *Aulacoseira*. There are, no doubt, good physiological reasons why this complex is necessary, but if so, then we should ask whether it is present in many other diatoms. We should also ask how much information of comparative morphological importance have we been missing by acid cleaning, which gives the type of picture of the inside surface of the valve shown in Fig. 2? Similar questions may also be asked of the diatotepum—a wholly organic component reported from a number of diatoms by von Stosch (1981, but see also Schulz et al. 1984), supported by thin sections, and illustrated here from *Odontella* and *Triceratium*. In *Odontella* there are several layers of what appear to be helicoidally arranged fibrils that recall in some respects the micrographs of *Subsilicea* by von Stosch and Reimann (1970), whereas in *Triceratium* there is a single layer with perforations beneath the areolae. These perforations resemble those beneath the ocellus in *Odontella* (von Stosch 1981, Fig. 19). Whether such perforations affect the passage of materials through the wall or not has yet to be established, and we do not yet know how widespread they are taxonomically. Nonetheless, these two examples reflect some of the variation existing in the diatotepum, particularly in centric diatoms. More thin sectioning is required here to obtain a fuller picture, but TEM studies have shown that more circumspect cleaning procedures may ensure more information from the SEM where, in the past, it has literally disappeared down the drain.

(3) How does the cell move?

After the problem of valve pattern, this is perhaps the most frequently posed and the most difficult to answer. However, with the elegant work of Edgar and others before her (Drum and Pankratz 1965; Hopkins and Drum 1966; Drum 1967), we may have come as close to a full explanation as we shall for some time. A combination of histochemical staining, fluorescence microscopy, and thin section work has demonstrated that in *Navicula cuspidata* actin filaments control the movement of mucopolysaccharide filaments that are produced by secretory vesicles along the length of the raphe slit. The cell is thus moved in the opposite direction (Edgar and Pickett-Heaps 1982, 1983; Edgar and Zavortink 1983). Similar filaments have been shown in other pennate diatoms, and Pickett-Heaps et al. (1991) propose a more general role for them in valve morphogenesis. Nevertheless, it remains to be shown how the fine control needed for change of direction and the high degree of synchrony so beautifully shown by *Bacillaria paxillifer* can be achieved, but an answer is more likely to come from physiological experiments than from microscopy.

(4) What are the phylogentic relationships of the major groups?

The phylogenetic relationships of the centrics, the araphid pennates, and the raphid pennates have been determined throughout the history of microscopy, but recent TEM studies of morphogenesis have made, and will continue to make, a significant contribution (Pickett-Heaps et al. 1991). For example, the position of the monoraphid group has been fundamentally changed from an exclusive position to one within the biraphid families in a recent classification based largely on studies of the developing "raphe" in the non-raphid valve mentioned above (Round et al. 1990). Much more needs to be done, but a major unanswered question concerns the position of the araphid group. Meaningful data is likely to come from molecular biology studies, but morphogenetic work is still needed on the genera.

(5) How has the diatom group as a whole evolved?

This final question has been partly answered through TEM work. The group is certainly monophyletic. Virtually all individuals replace a siliceous valve and a series of girdle bands at each cell division. They possess a unique method of locomotion in raphid genera and, astonishingly, the flagellum of the male gamete has been found to lack the central pair of microtubules in two genera, *Lithodesmium* (Manton and von Stosch 1966) and *Biddulphia* (Heath and Darley 1972). These findings need verification in other genera to establish how widespread the feature is within the centrics (motile gametes are absent from the raphid pennates). The proposals of Round and Crawford (1981), largely supported but significantly modified by Mann and Marchant (1989), that the diatoms evolved from scaly ancestors leaned heavily on the similarity of auxospore scales of a number of centric species to the simple structure of ribs radiating from an annulus in some developing centric valves. More thin sections of auxopores of both centrics and pennates will help answer question four, but other aspects of this question are more likely to come from molecular genetics.

In conclusion, despite the relatively small numbers of workers in the field, transmission electron microscopy and particularly thin sectioning has allowed us to make considerable advances and answer many of the questions posed above. Nevertheless, some questions remain, and new ones have been raised, but these are less likely to be resolved using one technique alone. There is clearly a greater need than ever for a holistic approach that combines whatever microscope technique may be needed with those of physiology, biochemistry, molecular genetics, and even those of ecology.

Acknowledgements

I am grateful to Rebecca Linstead for several of the micrographs from her investigation of *Aulacoseira*. This is AWI publication No. 460.

Literature Cited

ANDERSEN, R. A., L. K. MEDLIN AND R. M. CRAWFORD. 1986. An investigation of the cell wall components of *Actinocyclus subtilis (Bacillariophyceae). J. Phycol. 22:466–484.*

BLANK, G. S. AND C. W. SULLIVAN. 1983. Diatom mineralisation of silicic acid. VII. Influence of microtubule drugs on symmetry and pattern formation in valves of *Navicula saprophila* during morphogenesis. J. Phycol. 19:294–301.

BOROWITZKA, M. A. AND B. E. VOLCANI. 1978. The polymorphic diatom *Phaeo-dactylum tricornutum*: ultrastructure of its morphotypes. J. Phycol. 14:101–121.

BOYLE, J. A., J. D. PICKETT–HEAPS, AND D. B. CZARNECKI. 1984. Valve morphogenesis in the pennate diatom *Achnanthes coarctata*. J. Phycol. 20:563–573.

CHIAPPINO, M. L. AND B. E. VOLCANI. 1977. Studies on the biochemistry and fine structure of silica shell formation in diatoms. VII. Sequential cell wall development in the pennate *Navicula pelliculosa*. Protoplasma 93:205–221.

COX, E. J. 1981. The use of chloroplasts and other features of the living cell in the taxonomy of naviculoid diatoms. Pp. 115–133 *in* Proceedings of the sixth symposium on recent and fossil diatoms, R. Ross, ed. O. Koeltz, Koenigstein.

CRAWFORD, R. M. 1973. The protoplasmic ultrastructure of the vegetative cell of *Melosira varians* C. A. Agardh. J. Phycol. 9:50–61.

———. 1979. Filament formation in the diatom genera *Melosira* C.A. Agardh and *Paralia* Heiberg. Nova Hedwigia. Beih. 64:121–133.

CRAWFORD, R. M., H. M. CANTER, AND G. H. M. JAWORSKI. 1985. A study of two morphological variants of the diatom *Fragilaria crotonensis* Kitton using electron microscopy. Ann. Bot. 55:473–485.

CRAWFORD, R. M. AND F. E. ROUND. 1989. *Corethron* and *Mallomonas*—some striking morphological similarities. Pp. 295–305 *in* The Chromophyte Algae, problems and perspectives, B. S. C. Leadbeater, J. C. Green and W. A. Diver, eds. Oxford University Press.

CRAWFORD, R. M. AND A-M. SCHMID. 1986. Ultrastructure of silica deposition in diatoms. Pp. 291–314 *in* Biomineralisation in lower plants and animals. Systematics Association Special Volume No. 30, B. S. C. Leadbeater and R. Riding, eds. Oxford University Press.

DAVEY, M. C. AND R. M. CRAWFORD. 1986. Filament formation in the diatom *Melosira granulata*. J. Phycol. 22:144–150.

DAWSON, P. A. 1973. Observations on the structure of some forms of *Gomphonema parvulum* Kütz. III. Frustule formation. J. Phycol. 9:353–365.

DESIKACHARY, T. V. 1954. Electron microscope study of diatom wall structure. V. Trans. Amer. Microsc. Soc. 73:274–277.

DREBES, G. 1977. Sexuality. Pp. 250–283 *in* The Biology of Diatoms, D. Werner, ed. Blackwell, Oxford.

DRUM, R. W. 1967. Motility in Algae. III (abstract). J.Phycol. 3 (suppl.).

DRUM, R. W. AND H. S. PANKRATZ. 1964. Post mitotic fine structure of *Gomphonema parvulum*. J. Ultrastuct. Res. 10:217–223.

———. 1965. Locomotion and raphe structure of the diatom *Bacillaria*. Nova Hedwigia 10:315–317.

DRUM, R. W., H. S. PANKRATZ, AND E. F. STOERMER. 1966. Electron microscopy of diatom cells. *In* Diatomeenschalen im Elektronenmikroskopischen Bild. Teil VI, J–G. Helmcke and W. Krieger, eds. Cramer, Lehre.

EDGAR, L. A. AND J. D. PICKETT-HEAPS. 1982. Ultrastructural localisation of polysaccharides in the motile diatom *Navicula cuspidata*. Protoplasma 113:10–22.

———. 1983. The mechanism of diatom locomotion. I. An ultrastructural study of the motility apparatus. Proc. R. Soc. London B, 218:331–343.

———. 1984. Valve morphogenesis in the pennate diatom *Navicula cuspidata*. J. Phycol. 20:47–61.

EDGAR, L. A. AND M. ZAVORTINK. 1983. The mechanism of diatom locomotion II. Identification of actin. Proc. R. Soc. London B, 218:345–348.

FRYXELL, G. A. AND L. K. MEDLIN. 1981. Chain-forming diatoms: evidence of parallel evolution in *Chaetoceros*. Crypt. Algol. 2:3–29.

HEATH, I. B. AND W. M. DARLEY. 1972. Observations on the ultrastructure of the male gamete of *Biddulphia levis* Ehrenberg J. Phycol. 8:51–59.

HELMCKE, J–G. AND W. KRIEGER. 1953–1977. Diatomeenschalen im elektronenmikroskopischen Bild. Parts 1–10. Cramer, Vaduz.

HENDEY, N. I. 1959. The structure of the diatom cell wall as revealed by the electron microscope. J. Quekett Microsc. Soc. 5:147–175.

HOPKINS, J. T. AND R. W. DRUM. 1966. Diatom motility: an explanation and a problem. Br. phycol. Bull. 3:63–67.

HUSTEDT, F. 1945. Die Struktur der Diatomeen und des Elektronenmikroskops fur ihre Analyse. Archiv. f. Hydrobiologie. 41:315–332.

KOLBE, R. W. AND E. GOLZ. 1943. Elektronenmikroskopische Diatomeenstudien. Ber. d. Deutsch. Bot. Ges. 61:91–98.

LAUTERBORN, R. 1896. Untersuchungen ber Bau, Kernteilung und Bewegung der Diatomeen. W. Engelmann, Leipzig. 165 pp.

LI, C–W. AND B. E. VOLCANI. 1984. Aspects of silicification in wall morphogenesis of diatoms. Phil. Trans. Roy. Soc. Lond., B 304:519–528.

———. 1985a. Studies on the biochemistry and fine structure of silica shell formation in diatoms. VIII. Morphogenesis of the cell wall in a centric diatom *Ditylum brightwellii*. Protoplasma 124:10–29.

———. 1985b. Studies on the biochemistry and fine structure of silica shell formation in diatoms. IX. Sequential valve formation in a centric diatom *Chaetoceros rostratum*. Protoplasma 124:30–41.

———. 1985c. Studies on the biochemistry and fine structure of silica shell formation in diatoms. X. Morphogenesis of the labiate process in centric diatoms. Protoplasma 124:147–156.

MANN, D. G. 1983. Symmetry and cell division in raphid diatoms. Ann. Bot. 52:573–581.

MANN, D. G. AND H. J. MARCHANT. 1989. The origins of the diatom and its life cycle. *In* The Chromophyte Algae: problems and perspectives, B. S. C. Leadbeater, J. C. Green and W. A. Diver, eds. Oxford University Press, Oxford.

MANTON, I. AND H. A. VON STOSCH. 1966. Observations on the fine structure of the male gamete of the marine centric diatom *Lithodesmium undulatum*. J. Roy. Microsc. Soc. 85:119–134.

MANTON, I., K. KOWALLIK, AND H. A. VON STOSCH. 1969a. Observations on the fine structure and development of the spindle at mitosis and meiosis in a marine centric diatom (*Lithodesmium undulatum*) I. Preliminary survey of mitosis in spermatogonia. J. Microsc. 89:295–320.

———. 1969b. Observations on the fine structure and development of the spindle at mitosis and meiosis in a marine centric diatom (*Lithodesmium undulatum*) II. The early meiotic stages in spermatogenesis J. Cell Sci. 5:271–298.

———. 1970a. Observations on the fine structure and development of the spindles at mitosis and meiosis in a marine centric diatom (*Lithodesmium undulatum*) III. The later stages of meiosis I in male gametogenesis. J. Cell Sci. 6:131–157.

———. 1970b. Observations on the fine structure and development of the spindle at mitosis and meiosis in a marine centric diatom (*Lithodesmium undulatum*). IV. The second meiotic division and conclusion. J. Cell Sci. 7:407–443.

NAKAJIMA, T. AND B. E. F. VOLCANI. 1969. 3,4-Dihydroxyproline: a new amino acid in diatom cell walls. Science 164:1400–1401.

OKUNO, H. 1962. Electron microscopical study on fine structures of diatom frustules. XIX. Bot. Mag. Tokyo 75:119–126.

PICKETT-HEAPS, J. D. 1983. Valve morphogenesis and the microtubule centre in three species of the diatom *Nitzschia*. J. Phycol. 19:269–281.

———. 1987. Diatom mitosis: Implications of a model system. *In* Algal Development (Molecular and Cellular Aspects), W. Wiessner, D. G. Robinson, and R. C. Starr, eds. Springer–Verlag, Heidelberg.

PICKETT-HEAPS, J. D., A–M . M. SCHMID, AND L. A. EDGAR. 1991. The cell biology of diatom valve formation. *In* Progress in Phycological Research Vol. 7, F. E. Round and D. J. Chapman, eds. Biopress, Bristol.

PICKETT-HEAPS, J. D., A–M. M. SCHMID, AND D. H. TIPPIT. 1984. Cell division in diatoms. A translation of part of Lauterborn's Treatise of 1896 with some modern confirmatory observations. Protoplasma 120:132–154.

PICKETT-HEAPS, J. D., D. H. TIPPIT, AND J. A. ANDREOZZI. 1979. Cell division in the pennate diatom *Pinnularia*. IV. Valve morphogenesis. Biol. Cellulaire 35:199–206.

PICKETT-HEAPS, J. D., R. WETHERBEE, AND D. R. A. HILL. 1988. Cell division and morphogenesis of the labiate process in the centric diatom *Ditylum brightwellii*. Protoplasma 143:139–149.

REIMANN, B. E. F. 1964. Deposition of silica inside a diatom cell. Exp. Cell Res. 34:605–608.

ROSS, R., P. A. SIMS, AND G. R. HASLE. 1977. Observations on some species of the Hemiauloideae. Nova Hedwigia, Beih. 54:179–213.

ROTH, L. E. AND A. DE FRANCISCO. 1977. The marine diatom *Striatella unipunctata*. II. Siliceous structures and the formation of intercalary bands. Cytobiologie 14:207–221.

ROUND, F. E. AND R. M. CRAWFORD. 1981. The lines of evolution of the Bacillariophyta. I. Origin. Proc. Roy. Soc. London B 211:237–260.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms, Biology and Morphology of the Genera. Cambridge University Press. 747 pp.

SCHMID, A-M. M. 1980. Valve morphogenesis in diatoms: a pattern-related filamentous system in pennates and the effect of APM, cholchicine and osmotic pressure. Nova Hedwigia 33:811–847.

———. 1984a. Wall morphogenesis in *Thalassiosira eccentrica*: comparison of auxospore formation and the effect of MT inhibitors. Pp. 47–70 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

———. 1984b. Schalenmorphogenese in Diatomeen *in* Communications of Instit. Lightweight Structures. 28:300–317.

———. 1986a. Organization and function of cell structures in diatoms and their morphogenesis. Pp. 271–292 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard, ed. O. Koeltz, Koenigstein.

———. 1986b. Wall morphogenesis in *Coscinodiscus wailesii* Gran et Angst. II Cytoplasmic events of valve morphogenesis. Pp. 293–314 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard, O. Koeltz, Koenigstein.

SCHMID, A-M. M. AND D. SCHULTZ. 1979. Wall morphogenesis in diatoms: deposition of silica by cytoplasmic vesicles. Protoplasma 100:267–288.

SCHNEPF, E., G. DEICHGRABER, AND G. DREBES. 1980. Morphogenetic processes in *Attheya decora* (Bacillariophyceae, Biddulphiineae). Pl. Syst. Evol. 135:265–277.

SCHULZ, D. 1984. Das Schicksal von Silicalemma und Plasmalemma wahrend der Zellwandbildung bei *Coscinodiscus granii* Gough und *Thalassiosira eccentrica* (Ehrenb.) Cleve. Ber. d. Deutsch. Bot. Ges. 97:411–419.

SCHULZ, D., G. DREBES, H. LEHMANN, AND R. JANK-LODWIG. 1984. Ultrastucture of *Anaulus creticus* Drebes & Schultz with special reference to its reduced ocelli. Eur. J. Cell Biol. 33:43–51.

STOERMER, E. F., H. S. PANKRATZ, AND C. C. BOWEN. 1965. Fine structure of the diatom *Amphipleura pellucida*. II. Cytoplasmic fine structure and frustule formation. Am. J. Bot. 52:1067–1078.

STOSCH, H. A. VON. 1977. Observations on *Bellerochea* and *Streptotheca* including descriptions of three new planktonic diatom species. Nova Hedwigia, Beih. 54:113–166.

———. 1981. Structural and histochemical observations on the organic layers of the diatom cell wall. Pp. 231–252 *in* Proceedings of the 6th Symposium on Recent and Fossil Diatoms, R. Ross, ed. O. Koeltz, Koenigstein.

STOSCH, H. A. VON AND B. E. F. REIMANN. 1970. *Subsilicea fragilarioides* gen. et sp. nov., eine Diatomee (Fragilariaceae) mit vorwiegend organischer Membran. Nova Hedwigia, Beih. 31:1–36.

SUNDSTRÖM, B. G. 1984. The marine diatom genus *Rhizosolenia*. A new approach to the taxonomy. Doctoral dissertation (Lund BS/NBB–1008). 196 pp.

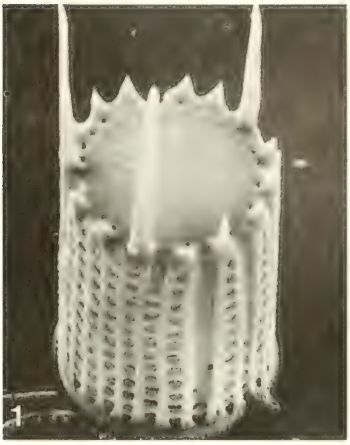
Explanation of Plates

Plate 1, Figs. 1–4

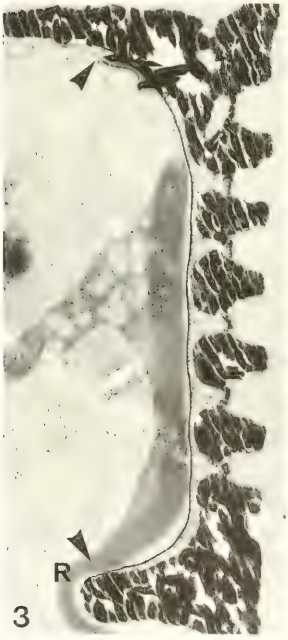
FIGURES 1–4. *Aulacoseira granulata.* FIGURE 1. Separation valve illustrating straight lines of pores on mantle and a non-porous valve face. × 3800. FIGURE 2. Inner surface of two sibling linking valves showing curved rows of pores. Arrows indicate internal apertures of two rimoportulae. Note clear image of areolae. See text for further explanation. × 3300. FIGURE 3. Thin section through mantle. Organo-silica complex extends from the "Ringleiste" (R) to the corner of the valve at the edge of the valve face, between the arrowheads. × 17,000. FIGURE 4. Section of interfacing sibling valves. Note point at which the complex fuses with valve face (arrows). × 10,000.

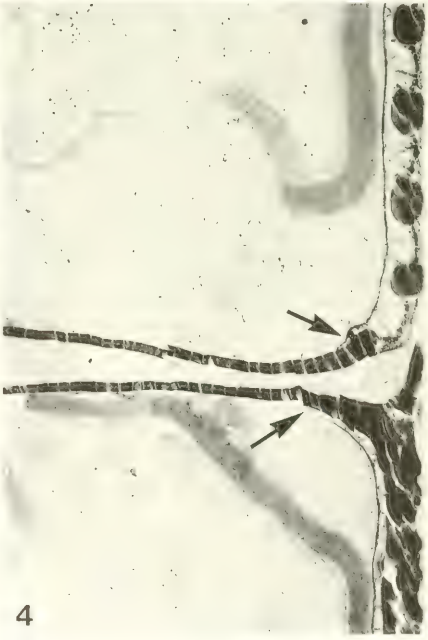
Plate 2, Figs. 5–8

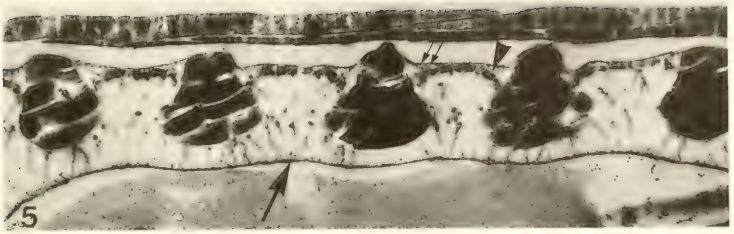
FIGURES 5, 6. *Aulacoseira granulata.* FIGURE 5. Detail of valve mantle overlain above by two series of girdle bands. Note fine branches of silica extending from the organic layer (arrow) to the pore plates (vela) of the areolae (arrowhead). There are also indications of silica and organic material outside the vela (double arrow). × 43,000. FIGURE 6. Similar section to Figure 5 but treated with dilute HF. × 48,000. FIGURE. 7. *Odontella* sp. Thin section of valve with diatotepum consisting of at least four layers of microfibrillar material apparently organized in a helicoidal arrangement. × 50,000. FIGURE. 8. Section of valve of *Triceratium* sp. Diatotepum extends underneath the valve surface but is thickest beneath areolae where pores are regularly found (arrows). × 41,000.

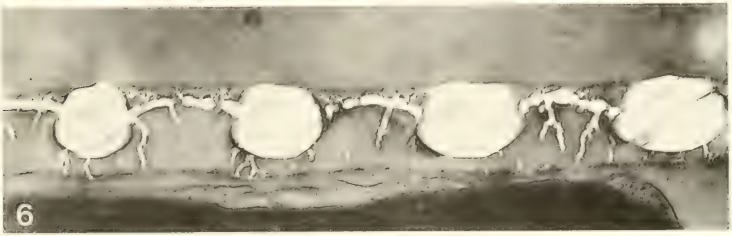

1

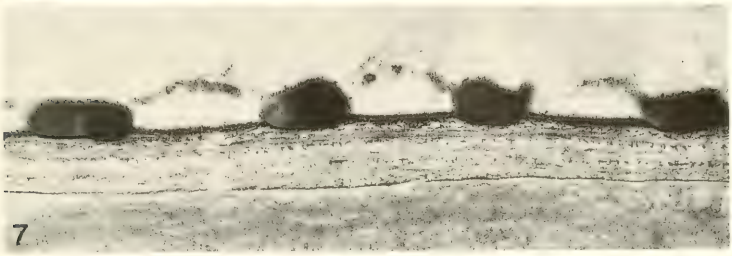
2

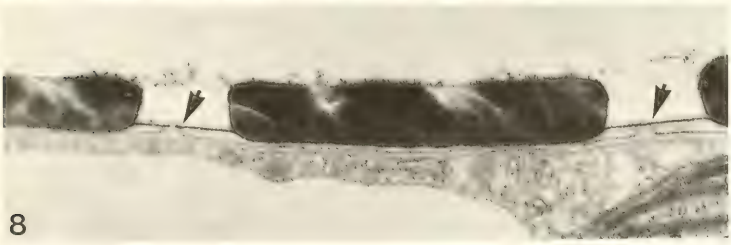

R
3


4


5


6


7


8

Diatoms, Or Their Chloroplasts, As Endosymbiotic Partners For Foraminifera

by

John J. Lee

Department of Biology, City College of CUNY,
Convent Avenue and 138th Street, New York, New York 10031

and

Department of Invertebrates, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024

with 5 plates

Abstract: Several families of larger foraminifera have representatives that harbor diatoms or the chloroplasts of diatoms as endosymbionts. The diatoms involved in these associations, all pennate taxa, are identified. Factors affecting the distributions of these symbiotic species and host-symbiont interactions are described. Foramineriferal symbioses with diatoms are compared to those involving other algal taxa.

Introduction

Foraminifera are a major group (220 families and 40,000, possibly as many as 60,000 fossil-described species but only 4,000 living species) of marine amoebae characterized by their distinctive granular reticulopodia (Fig. 1). Most have multichambered agglutinated or calcareous tests. Throughout their long evolutionary history (Cambrian to present) there have been families (~ 40) of ordinary sized foraminifera (50–500 μm) that have given rise to much larger descendants (1 mm–1 cm) that are given the general name **larger foraminifera**. The evolutionary occurrence of these protistan giants was not random but generally corresponded to polytaxic episodes in the geologic record (see Lee and Hallock 1987, and references cited therein), which were periods of global warming, reduced oceanic circulation, raised sea levels, and diminished planktonic productivity as a consequence of reduced nutrient input into the sea.

Because all the modern species of larger foraminifera are hosts for endosymbiotic algae, and because they are found in shallow tropical and semitropical seas where algal endosymbiosis is a common phenomenon (e.g., corals, giant clams, sea anemones), we infer that symbiosis was the driving force in the evolution of larger foraminifera (Lee and Hallock 1987; Lee et al. 1979a). The evidence to extend this hypothesis from the present

to extinct groups may be very difficult to obtain. While the tests of host foraminifera preserve well in the fossil record, their organic contents usually do not. Sporadic quick burial conditions during the fossilization procedure may hold the key to this question. A thin section and small samples of a phosphoric chert contained the remains of a paleozoic fusulinid larger foraminifer, *Pseudoschwagerina montanensis*, and hollow spherical remains that might have endosymbiotic algae (Lee and Hallock 1987). The whole question of which algal group (or groups) was (were) endosymbiotic in the extinct Paleozoic (Pennsylvanian -> Permian) fusulinids is intriguing.

Modern larger foraminifera as a group are the hosts for a wide diversity of algal types (reviewed in Lee and McEnery 1983, Lee and Anderson 1991). One family, Archaiadae, has species that are the hosts for chlorophytes (*Chlamydomonas* spp.). The foraminifera in another family, Peneroplidae, have endosymbiotic rhodophytes (*Porphridium purpureum*), and foraminifera in the family Soritidae bear endosymbiotic dinoflagellates (*Symbiodinium* spp. and *Amphidinium* sp.). Two families, Alveolinidae and Calcarinadae, which arose in the Cretaceous, and two other families Nummulitidae and Amphisteginidae, which arose in the Paleocene-Eocene, are hosts for endosymbiotic diatoms.

Diatoms as Endosymbionts

The individual diatom endosymbionts are located just below the expanded pore-rims in perforate foraminifera (Leutenegger 1977, 1983; Hansen and Burchardt 1977; McEnery and Lee 1981, Figs. 2–5). Several experiments, one using the vital dye neutral red, and the other, $H^{14}CO_3$, have indicated that the pores are physiologically active even though they have an organic lining (Berthold 1976; Leutenegger and Hansen 1979).

Although fine structural observations made as long ago as 1971 (Deitz-Elbrachter 1971) showed that diatoms were endosymbionts in some species of larger foraminifera, they could not be identified. Endosymbiotic diatoms within their hosts, in common with other foraminiferal endosymbionts, are naked protoplasts with highly reduced cell envelopes. Subsequent fine structural studies of diatom-bearing larger foraminifera confirmed the original observation that diatoms were endosymbionts and found some diversity in pyrenoid structure that suggested there might be more than one species of diatom involved in the symbiotic phenomenon (Leutenegger 1977, 1983, 1984; Hansen and Burchardt 1977; Berthold 1978; Schmalljohann and Rottger 1978). The abundance of larger foraminifera in modern seas and their contribution to deposition of $CaCO_3$ is not generally appreciated. On Kudaka Jima (Okinawa prefecture, Japan), living "star sands" (Calcarinids; Figs. 11, 13) are produced at a rate of 6×10^2g $CaCO_3$ $M^{-2}Y^{-1}$ (Sakai amd Nishihira 1981). Deposition rates are as high as kg $M^{-2}Y^{-1}$ in close proximity to coral reef margins (Hallock 1981). Fortunately the diatom endosymbionts were isolated in culture using methods that worked well with salt marsh diatoms (Lee et al. 1975), and they formed identifiable frustules (Lee et al. 1979b; Lee et al. 1980a, b). Since diversity of diatom symbiont species in the same hosts was recognized from the first isolations, many questions were raised. Were the endosymbiotic diatoms sequestered from those encountered by their hosts during their grazing? If that was the case, there should be some reflection of the internal diatom population in the external diatom assemblage. Are the endosymbiotic diatoms adaptive for hosts living at different depths or different seasons? Over the course of the past decade more than 3,000 specimens of larger foraminifera have been collected, carefully and aseptically brushed, washed, and then crushed, so that the diatom endosymbionts could be liberated, cultured, and identified. Results reported to date are from isolations from six species of larger foraminifera: *Amphistegina lessonii*, *A. lobifera*, *Heterostegina depressa*, *Borelis schlumbergerii* (Fig. 14), *Operculina ammonoides* (Fig. 12), and *Calcarina calcar*

(Fig. 11), mainly from the Gulf of Elat on the Red Sea, but also some specimens from the Indian Ocean, Hawaii, Palau, and the Great Barrier Reef (Lee et al. 1979, 1980a, b, 1989; Lee and Reimer 1983; Reimer and Lee 1984, 1988). Work on isolations from the Pacific "star sands" is still in progress.

Of 20 species of endosymbiotic diatoms isolated, all are small (< 10 µm), pennate species belonging to the genera *Fragilaria*, *Navicula*, *Nitzschia*, *Amphora*, *Achnanthes*, *Cocconeis*, and *Protokeelia* (Figs. 6–10). All of the endosymbiotic species are rare in the natural communities in which the foraminifera feed or have never been found other than as symbionts (Lee et al. 1989). Half of the endosymbionts found were new species or varieties. One species, *Navicula muscatinei*, has a very unusual life cycle for a diatom (Lee and Xenophontos 1989). It is the only one described thus far that has an autospore stage (Fig. 15). *Nitzschia frustulum* var. *symbiotica* was the most commonly isolated endosymbiont; it was found in 33.7% of the six hosts examined (Lee et al. 1989). Also very common in five of the hosts were *Nitzschia panduriformis* var. *continua* (14.5%), *Fragilaria shiloi* (9.9%), *Nitzschia laevis* (8.7%), and *Amphora roettgerii* (6%).

At every depth sampled, significant numbers of hosts harbored *N. frustulum* var. *symbiotica*, *N. laevis*, and *N. panduriformis* var. *continua*. In contrast, *F. shiloi* was rarely isolated from hosts at depths greater than 25 m. *Achnanthes macenerae*, *Protokeelia hottingeri*, and *Amphora sp.*, on the other hand, were only recovered in deeper waters (25 m). As a general rule (71% of the isolations), individual foraminifera usually hosted only one species of diatom at a time. In about 25% of the isolations, a second species was found; rarely three or more were isolated from the same host. Some of the endosymbiotic diatom species tended to be more common in particular hosts rather than others. *Nitzschia laevis* and *F. shiloi* were the most common endosymbionts in *Borelis schlumbergerii*; *N. laevis*, and *A. macenerae* were most common in *Operculina ammonoides*; and *N. frustulum* var. *symbiotica* was the most common in the population of *Calcarina calcar* from the Indian Ocean. No seasonal correlations of hosts and symbionts were found (Lee et al. 1989).

Several experimental studies attempted to answer the same questions by using a different approach. Specimens of *Amphistegina lessonii* were rendered nearly aposymbiotic by incubating them in tissue culture flasks containing 1 x 10^{-5}M DCMU anchored in a plastic raft at a shallow depth (5 m) in the Gulf of Elat. After five days the hosts had bleached and aliquots were: (1) fixed for fine structural studies (Koestler et al. 1985), (2) used in primary production studies, or (3) distributed into flasks containing mixtures of different species of endosymbiotic or free-living diatoms (Lee et al. 1983, 1986). Each mixture contained two endosymbiotic species and one non-symbiotic species. Ten different combinations of species were used. The flasks were then incubated in rafts anchored at 10-m and 20-m depth on the sea floor. The results suggested that some of the diatom species were selected (or were the most competitive) over others during the rebrowning of the hosts. None of the diatom species that were free-living isolates survived intracellularly in the foraminifera. By comparing the results of different combinations, *Nitzschia valdestriata* and *N. laevis* were the most successful endosymbionts and *F. shiloi* the least.

Since very few small pennate diatoms, out of a potential of several hundreds of small species found in the habitat of larger foraminifera, are involved in the endosymbiosis phenomenon, what are the "special properties" of these species that allow them to establish and maintain the relationship with their hosts? One of the more logical places to look for cell recognition properties is the cell envelope. Some initial progress along these lines has been reported (Lee et al. 1988a). Polyvalent antisera against the frustule fraction of each of three species of endosymbiotic diatoms, *N. panduriformis*, *F. shiloi*, and *A. ten-*

nerima, were raised in rabbits. The antisera were then reacted with the same and other species of endosymbiotic diatoms, with free-living diatoms, and with the frustule-less diatoms from freshly crushed diatom-bearing hosts.

By reacting the antisera first with one species and then with a second species, it was possible to show that the antisera contained antibodies that fell into that groups: (1) those that seemed to react with all the diatoms tested, (2) those that reacted only with the endosymbiotic species tested, and (3) those that reacted only with the particular species that was used as the antigen to raise the antisera in the rabbit. Goat anti-rabbit antibody conjugated with FITC was used to visualize the results in an epifluorescent microscope. The qualitative evidence that demonstrates that the endosymbiotic diatoms share some common surface antigens only piques curiosity and demands more quantitative and detailed probing by molecular techniques.

Nutritional studies of a number of endosymbiotic clones of *N. panduriformis*, *N. laevis*, *N. frustulum*, *N. valdestriata*, *A. tenerrima*, *Navicula reissii*, and *F. shiloi* suggested that all of the isolates required thiamine because the clones failed to grow on the second or third transfer to media without it (Lee et al. 1986). Biotin stimulated the growth of six of the eight clones tested. Only one clone (*N. frustulum*) was stimulated by vitamin B_{12}. Concentrations of NO_3 that supported optimal growth of the diatom clones spanned a range from 2 µm (*N. panduriformis*) to 2 mM (*N. valdestriata* and *F. shiloi*). At the depths in the Gulf of Elat, where most of the foraminifera were collected, the concentration of NO3 rarely exceeds 1 µg at 1-1 (Levanon-Spanier et al. 1979), a condition suggesting that even the foraminifera that host the diatoms with the lowest NO3 requirements must sequester and tightly recycle bound nitrogen, or that the systems are constantly nitrogen limited. The requirements for PO_4-3 gave a similar picture. *Nitzschia valdestriata* and *A. tenerrima* had the lowest requirements for optimal growth (1 µm) and *N. panduriformis*, *N. laevis*, and *N. reissii* the highest (100 µm). At the same depths the level of PO_4-3 rarely exceeds 0.3 µg at l^{-1}.

Field observations, field and laboratory experiments (Lee et al. 1980a, d; Zmiri et al. 1974) and growth experiments (Hallock 1981; Rottger 1972, 1976) of intact host/symbiont systems suggested that there were optimum ranges of light intensities and spectral qualities for growth, calcification, and primary production. Respirometry was used to test the responses of four species of diatom endosymbionts: *N. laevis*, *N. panduriformis*, *N. valdestriata*, and *F. shiloi* (Lee et al. 1982). The clones tested were photoinhibited at high light intensities and did well at moderately low light (175 µW cm^{-2}). Photocompensation points of these clones were at a light level that approximated 2% of the light measured at 1 m in the spring at Elat. If the algae were free (that is, not inside the foraminiferal shell) photocompensation depth for the clones tested would be reached between 40–50 m.

The depth ranges of diatom-bearing larger foraminifera are quite interesting. Some species (e.g., *Heterostegina depressa* and *Operculina ammonoides*) seem to occupy wide ranges of depth (Leutenegger 1983). However, when this is examined more closely, the statement needs qualification. For example, at shallow depths *H. depressa* is found on the shady sides of tide pools (Röttger 1972) but in the Gulf of Elat it is found in deeper water (30–40 m). Several simple behavioral studes have shown phototaxis in diatom-bearing larger foraminifera (Zmiri et al. 1974; Lee et al. 1980a). *Amphistegina lessonii* was phototaxic at photonic fluxes between 10^{11}-10^{15} photons cm^{-2} S^{-1} and unresponsive at lower light levels. The action spectrum for this response peaked near 500 nm (Zmiri et al 1974). *Amphistegina lobifera* was positively phototaxic at an incident illumination between 0.1–1 klx and negatively phototaxic at higher light levels (~4 klx) (Lee et al. 1980a). These phototaxic responses help explain the distribution of some species, for example

Operculina ammonoides, just below the surface of the sediment at 35–40 m in Elat and on the surface of the sediment when it is shaded by patches of *Halophila stipulacea*. Other diatom-bearing larger foraminifera seem to have more restricted depth ranges (reviewed in Leutengger 1983; Reiss and Hottinger 1984). Some diatom-bearing species (e.g., *Baculogypsina sphaerulata* and *Calcarina calcar*) are found only in shallow waters; other species (e.g., *Heterocyclina tuberculata* and *Cyclopeus carpenteri*) are only found in deeper (70 m) waters.

The growth rates of diatom-bearing species of larger foraminifera, which have been studied in the laboratory, are correlated with light (Röttger 1972, 1974; Muller 1978). None of the species tested will grow in the dark, even if they are well fed. *Heterostegina depressa* was the first of these diatom-bearing species to be studied in this respect (Röttger 1972, 1974). This species survives and grows well in the absence of any obvious concentration of food if it is incubated in the light. Both *H. depressa* and *Amphistegina lessonii* grew best at 600–800 lux (~ 12–16 μE m^{-2} S^{-1}) (Röttger et al. 1980). Slightly higher light levels (14–40 μE m^{-2} S^{-1}) gave the maximum growth rate for other Hawaiian clones of *A. lessonii* (Hallock et al. 1986). The light saturation level for clones of *A. gibbosa* from the Caribbean was also between 14 and 40 μE $m^{-2}S^{-1}$. Populations grown at 6.4 and 3.9 μE $m^{-2}S^{-1}$ had lighter, thinner, and flatter tests than those at higher light levels (Hallock et al. 1986).

Primary production, as measured by ^{14}C incorporation in *Amphistegina lessonii* and *A. lobifera* was 1.95×10^{-5} mg ^{14}C h^{-1} foraminifer $^{-1}$ and 2.9×10^{-5}mg^{14}C h^{-1} foraminifer^{-1} respectively (Hallock 1981; Muller 1978). The role of symbiont-fixed carbon in the overall carbon budgets of larger foraminifera seems to vary widely. As mentioned earlier, symbiont-fixed carbon seems to satisfy the overall carbon budget of the diatom-bearing species *Heterostegina depressa* (Röttger 1972, 1974). Feeding by these species seems to supply fixed nitrogen, phosphorus, and, perhaps, micronutrients and vitamins to the foraminiferan/symbiont system. The same may also be true for *Amphistegina spp.* (Lee et al. 1988b; Kuile et al. 1987). This aspect of other species of diatom-bearing larger foraminifera is unknown. However, studies of symbiont-bearing planktonic foraminifera and dinoflagellate-bearing larger foraminifera show that feeding is the major source of fixed carbon for these types of associations (Bé et al. 1981; Lee and Bock 1976).

The transfer of symbiont-fixed carbon to their hosts has not been studied in detail. Fine structural studies of a number of species of chlorophyte-bearing and dinoflagellate-bearing hosts have shown starch grains packed in symbionts and distributed in the host's cytoplasm (Leutenegger 1977, 1983; Müller-Merz and Lee 1976). How they get from one to the other is inferential. They may be released from digested or autolyzed cells, or they may be exocytosed. With the exception of the red algal symbionts, all symbionts in the foraminifera are surrounded by their own cell membrane and a symbiosome (or symbiont vacuole). The starch would have to pass through both. Fine structural studies of *Peneroplis* and its endosymbiotic red alga, *Porphyridium purpureum*, seem to suggest that polysaccharide sheath fibrils are passed from the symbiont directly into the cytoplasm of the host (Lee 1990). Fine structure cannot give an easily grasped, quantitative, dynamic answer to the transfer question. Chromatographic techniques were used to separate and identify ^{14}C tracer- labeled photosynthates in six foraminiferal/algal associations (Kremer et al. 1980). A large percentage of the label in the three diatom-bearing species tested, *A. lobifera*, *A. lessonii*, and *H. depressa*, was found in lipids (51, 31 and 33% respectively) and glycerol (6, 5 and 11%). Further work along these lines with careful separation of symbionts from host cytoplasm by differential centrifugation could be quite useful in characterizing pathways of carbon flow. Host digestion of symbionts and/or symbiont autolysis are possible pathways of energy flow from the symbionts to the hosts that have not been carefully

examined. Evidence for flow of carbon from ^{14}C tracer-labeled food to the symbionts in *Amphistegina lobifera* and *Amphisorus hemprichii* was clearly demonstrated in radioautographs (Lee et al. 1988b).

Endosymbiots isolated from a variety of algal/invertebrate systems are stimulated to release metabolites in the presence of host homogenates (reviewed by Trench 1979). A sterile homogenate from crushed whole *Amphistegina* was also effective in stimulating the release of ^{14}C labeled photosynthate from the log phase axenic endosymbiotic diatom clones tested (*N. valdestriata*, *N. laevis*, *N. panduriformis*, *N. frustulum* var. *symbiotica*, *A. tenerrima*, *F. shiloi*, and *Navicula hanseniana*). The increase of release ranged from 190 to 9,000% (25–76% total carbon fixed, not corrected for respiration; Lee et al. 1984). The host homogenate also stimulated a control, a clone of *Amphora sp.* that was isolated as an epiphyte in a salt marsh. The authors (Lee et al. 1984) were quite cautious about interpreting their results without further separation and categorization of the active factor(s). In varying degrees, the host homogenate had other effects on the growing and dividing diatoms; it interfered with formation of new frustules (Figs. 16–18). *Fragilaria shiloi* was the most affected species (Figs. 16, 18). New cells were protoplasts with little or no vestiges of frustules. Since the endosymbionts are all protoplasts in their hosts (Fig. 3) this seems a very promising topic for future study of host/symbiont interactions.

Diatom Chloroplasts as Endosymbionts

A review of the relationships between diatoms and foraminifera must consider the diatom-chloroplast husbanding (or sequestering) foraminifera (Figs. 19, 20). Some members (perhaps many, or all) of three families, Elphidiidae, Nonionidae and Rotaliellidae, are known to retain functional chloroplasts of some of the algae they partially consume. The nonionids and elphidiids are morphologically very complex. Their apertures, the principal opening from which most foraminiferal pseudopodia emerge, are very reduced. In the elphidiids the sutures between chambers have funnel-like openings, fossae, through which the pseudopods emerge (Fig. 19). The fossae are lined with tooth- or comb-like projections that seem to act like sieves. Microalgae trapped by the reticulopodial web are transported back to those sieved, depressed openings where digestion takes place (Lee et al. 1991). Here frustules remain as the chloroplasts are extracted from partially digested diatoms. The fossae are openings of an elaborate canal system that is connected to every chamber (diagram in Lee and Hallock 1987). The relationship (if there is any) of the canal systems in elphidids to the chloroplast husbandry phenomenon has not yet been rigorously studied. The number of chloroplasts husbanded by the nonionids and elphiidids is quite high. For example, several species, *Elphidium williamsoni*, *E. excavatum*, and *Haynesina germanica*, collected from the shallow waters of Limfjorden (Denmark), sequestered respectively 9.7 ($\pm$ 4.9) $\times 10^3$, 1.2 $\times 10^3$, and 5.2 ($\pm$ 1.6) $\times 10^3$) chloroplasts per organism (Lopez 1979). Similar numbers have been reported for members of the same families collected at Plymouth, England; Falmouth, Massachusetts; Southampton, New York; Elat, Israel; and Mombasa, Kenya (Lee et al. 1988c; Lee and Lee 1990). Primary production calculated on an organic dry weight basis is as high in chloroplast-sequestering species as it is in larger foraminifera with whole diatoms (Lopez 1979; Lee et al. 1988b). For example, *Elphidium crispum* and *Heterostegina depressa* were both collected by hand in the same sample at 38 m at Wadi Taba on the Red Sea. Specimens of *E. crispum* fixed 1.5 µg C mg foraminiferal dry-weight^{-1} 48 h^{-1} while specimens of *Heterostegina depressa*, a diatom-bearing species, fixed slightly less (1.28 µg C mg foraminiferal dry-weight^{-1} 48 h^{-1}) (Lee et al. 1988c).

Fine structural studies and photosynthetic pigment analyses have provided further information on the nature of chloroplast donors and the relative preservation state of the

chloroplasts and their pigments (Lopez 1979; Knight and Mantoura 1985; Lee et al. 1988c). The chloroplasts are in various states of preservation but most appear to be normal diatom chloroplasts surrounded by a host vacuole. HPLC and two-dimensional chromatography showed typical diatom pigments; chlorophylls a and c, fucoxanthin, diatoxanthin and, as could be expected, some phaeophytins a and c (Lopez 1979; Knight and Mantoura 1985). Several studies have attempted to measure the life of sequestered chloroplasts, factors that affect chloroplast longevity, and selectivity in chloroplast donors (Lopez 1979; Lee and Lee 1990). Results suggested that the phenomenon needs to be studied on a case-by-case basis. For example, Lopez (1979) calculated that under normal light/dark conditions *E. williamson* must eat at least 65 chloroplasts individual^{-1} h^{-1} while *H. germanica* needed to consume only 20 individual^{-1}h^{-1}. When juvenile *H. germanica* were fed a mixture of *Navicula menisculus* and *Amphora tenerrima*, they sequestered a steady state population of 80 chloroplasts in the light and half as many when incubated in the dark (Lee and Lee 1990). Some quality aspects of chloroplast retention have been shown in experiments in which only one algal species was available. The chloroplasts of *Chlorella* were sequestered at very low numbers by *Elphidium crispum* from Drake's Island in Plymouth harbor, England. On the other hand, the number of chloroplasts sequestered by populations fed only *Cocconeis placentula* or *Amphora* sp. were approximately 160–180 individual^{-1} (Lee and Lee 1990). The initial chloroplast loss of starved elphidiids maintained in the light was rapid ($T_{1/2}$ 2 weeks) and then became more gradual ($T_{1/2}$ 5 weeks; Lee and Lee 1990).

While much is known about the diatom-bearing and diatom chloroplast sequestering foraminifera, in truth, almost every aspect of the phenomena needs deeper probing. Among the more interesting aspects I look forward to working on in the next few years are the following questions: Can we detect the differences between small pennate diatoms that are endosymbionts and those that are not? Are there any antigenic similarities between sequestered chloroplasts and endosymbiotic envelopes? What are the metabolites passed from the diatoms to their hosts? How are diatom population numbers regulated in their hosts? I hope others will join us in examining these interesting and unusual diatom-involved phenomena.

Literature Cited

BÉ, A. W. H., D. A. CARON, AND O. R. ANDERSON. 1981. Effects of feeding frequency on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture. J. Mar. Biol. Assoc. U. K. 61:257–277.

BERTHOLD, W. U. 1976. Ultrastructure and function wall perforations in *Patellina corrugata* Williamson, Foraminifera. J. Foraminiferal Res. 6:22–29.

———. 1978. Ultrastrukturanalyse der endoplasmatischen Algen von *Amphistegina lessonii* d'Orbigny, Foraminifera (Protozoa) und ihre systematische Stellung. Arch. f. Protistenk. 120:16–62.

DIETZ-ELBRACHTER, G. 1971. Untersuchungen über die Zooxanthellen der Fora-minifere *Heterostegina depressa* d'Orbigny 1826. Meteor Forsch. Ergeb. 6:41–47.

HALLOCK, P. 1981. Light dependence in *Amphistegina*. J. Foraminiferal Res. 11:40–46.

HALLOCK, P., L. B. FORWARD AND H. J. HANSEN. 1986. Influence of environment on the test shape of *Amphistegina*. J. Foraminiferal Res. 16:224–231.

HANSEN, H. J. AND B. BUCHARDT. 1977. Depth distribution of *Amphistegina* in the Gulf of Elat. Utrecht Micropaleont. Bull. 1:225–239.

KNIGHT, R. AND R. F. C. MANTOURA. 1985. Chlorophyll a and carotenoid pigments in foraminifera and their symbiotic algae: analysis by high performance liquid chromatography. Mar. Ecol. Prog. Ser. 23:241–249.

KOESTLER, R. J., J. J. LEE, J. REIDY, R. P. SHERYLL AND X. XENOPHOTOS. 1985. Cytological investigation of digestion and re establishment of symbiosis in the larger benthic foraminifer *Amphistegina lessonii*. Endocytobiosis Cell Res. 2:21–54.

KREMER, B. P., R. SCHMALJOHANN AND R. RÖTTGER. 1980. Features and nutritional significance of photosynthates produced by unicllular algae symbiotic with larger foraminifera. Mar. Ecol. Prog. Ser. 2:225–228.

KUILE, B. TER, J. EREZ AND J. J. LEE. 1987. The role of feeding in the metabolism of larger symbiont-bearing foraminifera. Symbiosis 4:335–350.

LEE, J. J. 1990. Fine structure of the rhodophycean *Porphyridium purpureum* in situ in *Peneroplis pertusus* (Forskol and *P. acicularis* (Batsch) and in axenic culture. J. Foraminiferal Res. 20:162–169.

LEE, J. J. AND O. R. ANDERSON. 1991. The biology of foraminifera. Academic Press, London.

LEE, J. J. AND W. D. BOCK. 1976. The importance of feeding in two species of soritid foraminifera with algal symbionts. Bull. Mar. Sci. 26:530–537.

LEE, J. J., Y. CHAN, AND A. LAGZIEL. 1988a. An immunofluorescence approach toward the identification of endosymbiotic diatoms in several species of larger foraminifera. Pp. 230–241 *in* Immunochemical approaches to coastal estuarine and oceanographic questions, C. M. Yentsch, F. C. Mague and P. K. Hogan, eds. Springer-Verlag, NY.

LEE, J. J., J. EREZ, B. TER KUILE, A. LAGZIEL AND S. BURGOS. 1988b. Feeding rates of two species of larger foraminifera *Amphistegina lobifera* and *Amphisorus hemprichii*, from the Gulf of Eilat (Red Sea). Symbiosis 5:61–102.

LEE, J. J., J. EREZ, M. E. MCENERY, A. LAGZIEL AND X. XENOPHOTOS. 1986. Experiments on persistence of endosymbiotic diatoms in the larger foraminifer *Amphistegina lessonii*. Symbiosis 1:211–226.

LEE, J. J., W. W. FABER, JR. AND R. E. LEE. 1991. Granular reticulopodal digestion—a possible preadaptation to benthic foraminiferal symbiosis? Symbiosis, in press.

LEE, J. J. AND P. HALLOCK. 1987. Algal symbiosis as the driving force in the evolution of larger foraminifera. Ann. N. Y. Acad. Sci. 503:330–347.

LEE, J. J., E. LANNERS, AND B. TER KUILE. 1988. Retention of chloroplasts by the foraminifer *Elphidium crispum*. Symbiosis 5:45–60.

LEE, J. J. AND R. E. LEE. 1990. Chloroplast retention in elphidids (Foraminifera) Pp. 215–220 *in* Endocytobiology IV, P. Nardon, V. Gianinazzi-Pearson, A. M. Grenier, L. Margulis and D. C. Smith, eds. Institut National de la Recherche Agronomique, Paris.

LEE, J. J. AND M. E. MCENERY. 1983. Symbiosis in foraminifera. Pp. 36–68 *in* Algal Symbiosis, L. J. Goff, ed. Cambridge Univ. Press, Cambridge.

LEE, J. J., M. E. MCENERY, AND J. GARRISON. 1980a. Experimental studies of larger foraminifera and their symbionts from the Gulf of Elat on the Red Sea. J. Foraminiferal Res. 10:31–47.

LEE, J. J., M. E. MCENERY, E. KAHN, AND F. SCHUSTER. 1979a. Symbiosis and the evolution of larger foraminifera. Micropaleontology 25:118–140.

LEE, J. J., M. E. MCENERY, R. L. KOESTLER, M. J. LEE, J. REIDY, AND M. SHILO. 1983. Experimental studies of symbiont persistence in *Amphistegina lessonii*, a diatom-bearing species of larger foraminifera from the Red Sea. Pp. 487–514 *in* Endocytobiology II, H. E. A. Schenk and W. Schwemmler (eds.). Walter de Gruyter and Co., Berlin.

LEE, J. J., M. E. MCENERY, B. TER KUILE, J. EREZ, R. RÖTTGER, R. F. ROCKWELL, W. W. FABER, JR., AND A. LAGZIEL. 1989. Identification and distribution of endosymbiotic diatoms in larger foraminifera. Micropaleontology 35:353–366.

LEE, J. J., M. E. MCENERY, M. J. LEE, J. REIDY, J. GARRISON, AND R. ROTTGER. 1980b. Algal symbionts in larger foraminifera. Pp. 113–124 *in* Endocytobiology 1, W. Schwemmler and H. E. A. Schenk, eds. Walter de Gruyter and Co., Berlin.

LEE, J. J., M. E. MCENERY, R. ROTTGER, AND C. W. REIMER. 1980c. The isolation, culture and identification of endosymbiotic diatoms from *Heterostegina depressa* d'Orbigny and *Amphistegina lessonii* d'Orbigny (larger foraminifera) from Hawaii. Bot. Mar. 23:297–302.

LEE, J. J., M. E. MCENERY, M. SHILO, AND Z. REISS. 1979b. Isolation and cultivation of diatom endosymbionts from larger foraminifera (Protozoa). Nature 280:57–58.

LEE, J. J. AND C. W. REIMER. 1983. Isolation and identification of endosymbiotic diatoms from larger foraminifera of the Great Barrier Reef, Australia, Makapuu Tide Pool, Oahu, Hawaii, and the Gulf of Elat, Israel, with the description of three new species *Amphora roettgerii*, *Navicula hanseniana*, and *Nitzschia frustulum* variety *symbiotica*. Pp. 327–343 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

LEE, J. J., C. W. REIMER, AND M. E. MCENERY. 1980d. The identification of diatoms isolated as endosymbionts from larger foraminifera from the Gulf of Elat (Red Sea) and the description of 2 new species, *Fragilaria shiloi*, sp. nov. and *Navicula reisii* sp. nov. Bot. Mar. 23:41–48.

LEE, J. J., N. M. SAKS, F. KAPIOUTOU, S. H. WILEN, AND M. SHILO. 1984. Effects of host cell extracts on cultures of endosymbiotic diatoms from larger foraminifera. Mar. Biol. 82:113–120.

LEE, J. J. AND X. XENOPHOTOS. 1989. The unusual life cycle of *Navicula muscatinei*. Diatom Res. 4:69–77.

LEE, M. J., R. ELLIS, AND J. J. LEE. 1982. A comparative study of photoadaptation in four diatoms isolated as endosymbionts from larger foraminifera. Mar. Biol. 68:193–197.

LEUTENEGGER, S. 1977. Ultrastructure de foraminiferes perfores et imperfores ainsi que de leurs symbiotes. Cah. Micropaleont. 3:1–52.

———. 1983. Specific host-symbiont relationship in larger foraminifera. Micropaleontology 29:111–125.

———. 1984. Symbiosis in benthic foraminifera: specificity and host adaptations. J. Foraminiferal Res. 14:16–35.

LEUTENEGGER, S. AND H. J. HANSEN. 1979. Ultrastructural and radiotracer studies of pore-function in foraminifera. Mar. Biol. 54:11–16.

LEVANON-SPANIER, I., E. PADAN, AND Z. REISS. 1979. Primary production in a desert-enclosed sea—the Gulf of Elat (Aqaba), Red Sea. Deep Sea Res. 26:673–685.

LOPEZ, R. 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomic affinity, viability and persistence. Mar. Biol. 53:201–211.

MCENERY, M. E. AND J. J. LEE. 1981. Cytological and fine structural studies of three species of symbiont-bearing larger foraminifera from the Red Sea. Micropaleontology 27:71–83.

MULLER, P. H. 1978. ^{14}Carbon fixation and loss in a foraminiferal-algal symbiont system. J. Foraminiferal Res. 8:35–41.

MÜLLER-MERZ, E. AND J. J. LEE. 1976. Symbiosis in the larger foraminiferan *Sorites marginalis* (with notes on *Archaias* spp.). J. Protozool. 23:390–396.

REIMER, C. W. AND J. J. LEE. 1984. A new pennate diatom: *Protokeelia hottingeri* gen. et sp. nov. Proc. Acad. Nat. Sci. Phila. 136:194–199.

———. 1988. New species of endosymbiotic diatoms (Bacillariophyceae) inhabiting larger foraminifera in the Gulf of Elat (Red Sea), Israel. Proc. Acad. Nat. Sci. Phila. 140:339–351.

REISS, Z. AND L. HOTTINGER. 1984. The Gulf of Aqaba. Springer-Verlag, NY.

RÖTTGER, R. 1972. Die Bedeutung der Symbiose von *Heterostegina depressa* (Foraminifera, Nummulitidae) fur hohe Siedlungsdichteund Karbonatproduktion. Abh. Deut. Zool. Gesch. 65:43–47.

———. 1974. Larger foraminifera: reproduction and early stages of developement in *Heterostegina depressa*. Mar. Biol. 26:5–12.

———. 1976. Ecological observations of *Heterostegina depressa* (Foraminifera, Nummulitidae) in the laboratory and in its natural habitat. Maritime Sed. Spec. Pub. 1:75–80.

RÖTTGER, R., A. IRWAN, R. SCHMALJOHANN, AND L. FRANZISKET. 1980. Growth of the symbiont-bearing foraminifera *Amphistegina lessonii* D'Orbigny and *Heterostegina depressa* D'Orbigny (Protozoa). Pp. 125–132 *in* Endocytobiology 1, W. Schwemmler and H. E. A. Schenk, eds. Walter de Gruyter and Co., Berlin.

SAKAI, K. AND M. NISHIHIRA. 1981. Population study of the benthic foraminifera *Baculogypsina sphaerulata* on an Okinawan reef flat and preliminary estimation of its annual production. Proc. Fourth Int. Coral Reef Symp. 2:763–766.

SCHMALJOHANN, R., AND R. ROTTGER. 1978. The ultrastructure and taxonomic identity of the symbiotic algae of *Heterostegina depressa* (Foraminifera: Nummunlitidae). J. Mar. Biol. Assoc. U. K. 58:227–237.

TRENCH, R. K. 1979. The cell biology of plant-animal symbioses. Ann. Rev. Plant Phys. 30:485–532.

ZMIRI, A., D. KAHAN, S. HOCHSTEIN, AND Z. REISS. 1974. Phototaxis and thermotaxis in some species of *Amphistegina (Foraminifera)*. J. Protozool. 21:133–138.

Explanation of Plates

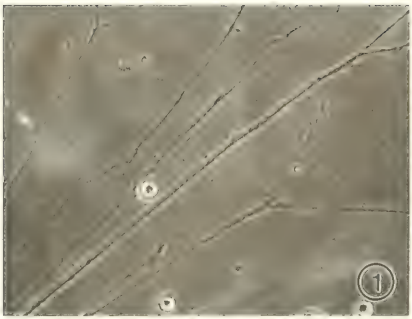
Plate 1, Figs. 1–5
FIGURE 1. Granulareticulopodia characteristic of a foraminiferan. LM, Phase contrast. 1000x. FIGURE 2. Endosymbiotic diatoms (D) in the pockets formed by pore rims inside test (shell) of a foraminifera. The organic liner of the pore (P) remains after test has been dissolved. TEM. Scale bar = 10 µm. FIGURE 3. Endosymbiotic diatom in a pore rim. Symbiosome membrane (arrow) surrounds cell; note absence of a frustule. TEM. 24,000x. FIGURE 4. Fragment of a perforate foraminiferan test showing pores (arrow) in cross section and cup-like inner pore rims. SEM. Scale bar = 10 µm. FIGURE 5. Fragment of perforate foraminiferan test illuminated and inclined at an angle to emphasize cup-like apsects of pore rims. SEM. Scale bar = 20 µm.

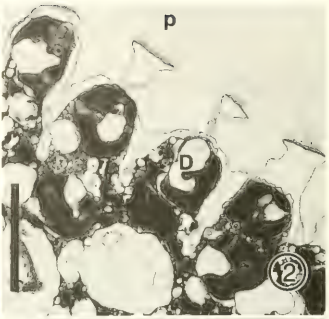
Plate 2, Figs. 6–10
FIGURES 6–10. Representative endosymbiotic diatoms. FIGURE 6. *Nitzschia frustulum* var. *symbiotica* (left); *Fragilaria shiloi* (right). Scale bar = 4 µm. FIGURE 7. *Cocconeis andersonii*. Scale bar = 2 µm. FIGURE 8. *Navicula muscatinei*. Scale bar = 2 µm FIGURE 9. *Protokeelia hottingeri*. Scale bar = 4 µm. FIGURE 10. *Nitzschia valdestriata*. Scale bar = 4 µm. All figures SEM.

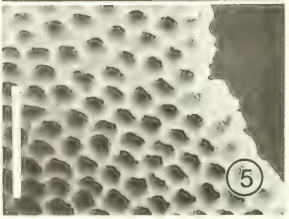
Plate 3, Figs. 11–13
FIGURES 11–13. Representative foraminifera hosts of endosymbiotic diatoms. FIGURE 11. Pacific "star sand," *Calcarina calcar*. Scale bar = 400 µm. FIGURE 12. A modern nummulite (coin-shaped foraminiferan) from the Red Sea, *Operculina ammonoides*. Scale bar = 1 mm. FIGURE 13. Indo-Pacific "star sand," *Calcarina spengleri*. Scale bar = 400 µm. FIGURE 14. A "roller-shaped" modern imperforate foraminifer, *Borelis schlumbergii*. Scale bar = 200 µm. All figures SEM.

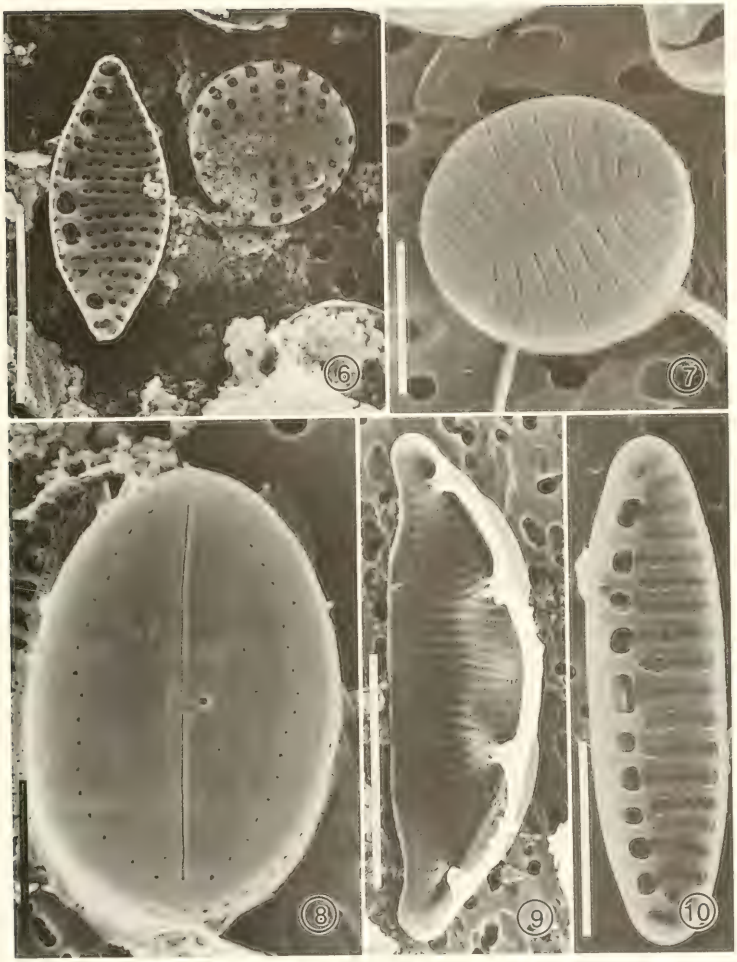
Plate 4, Figs. 14–18
FIGURES 15–18. Endosymbiotic diatom species. FIGURE 15. Putative autospore of *Navicula muscatinei*. From study by Lee and Xenophontos (1989). Scale bar = 10 µm. FIGURES 16–18 are from log phase cultures treated with sterile homogenates of host cells (Lee et al. 1984). FIGURE 16. *Fragilaria shiloi* with a partially formed frustule. Scale bar = 4 µm. FIGURE 17. *Nitzschia frustulum* var. *symbiotica* with partially formed frustule. Scale bar = 4 µm. FIGURE 18. *F. shiloi* that has divided twice during incubation with host homogenate. Note no new frustule elements have been formed during this interval. Scale bar = 4 µm. All figures SEM.

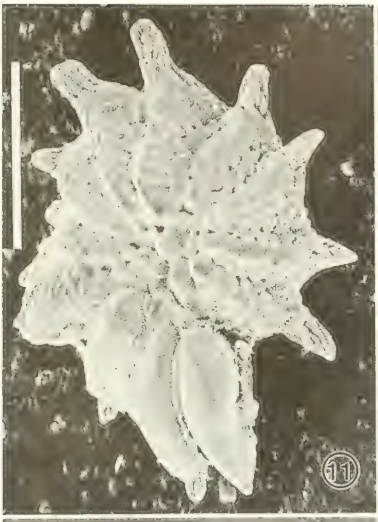
Plate 5, Figs. 19–21
FIGURES 19–21. Chloroplast-sequestering species of foraminifera. FIGURE 19. *Elphidium crispum* from the Indian Ocean at Mombasa, Kenya. SEM. Scale bar = 200 µm. FIGURE 20. *Haynesina germanica* from the Greater Sippewisett salt marsh, Falmouth, Massachusetts. SEM. Scale bar = 100 µm. FIGURE 21. Sequestered chloroplasts (c) in a section of a chamber of *E. crispum* from the Indian Ocean at Mombasa, Kenya. TEM. 11,500x.

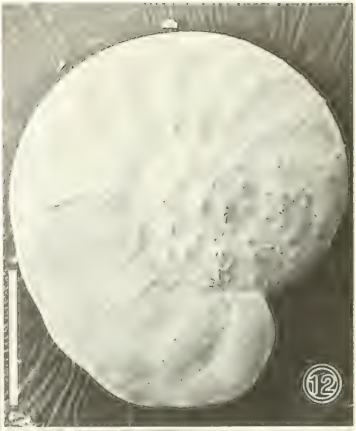



p
D



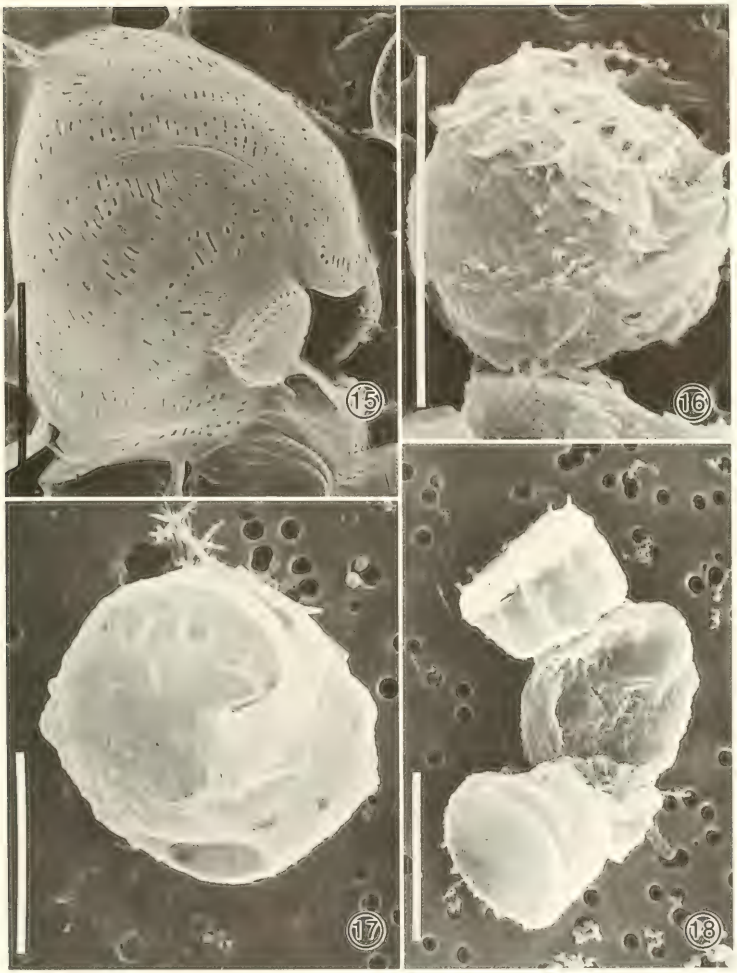

6
7
8
9
10

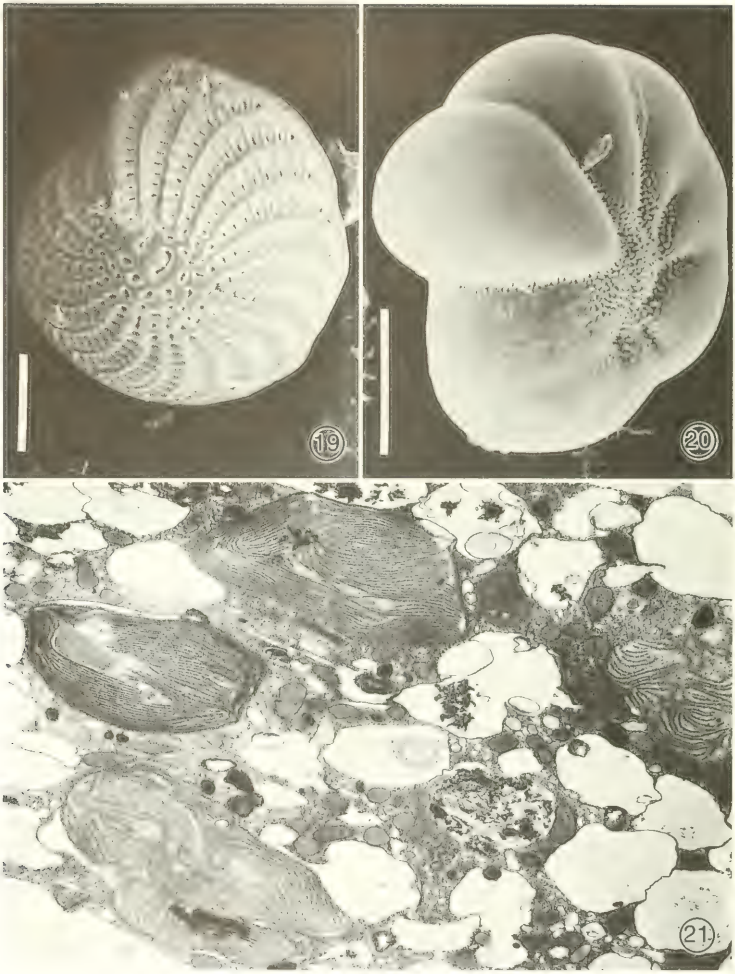

11


12

13

14


15
16
17
18


19
20
21

Asteromphalus sarcophagus Wallich and Other Species of the Genus Off the Coast of Chile

by

P. S. Rivera and H. L. Barrales

Department of Botany, University of Concepción,
P. O. Box 2407, Ap. 10, Concepción, Chile

with 2 tables and 4 plates

Abstract: *Asteromphalus* Ehrenberg is the only genus of the family Asterolampraceae found along the Chilean coast. The most common species reported from Chile, both from coastal and oceanic waters, is *A. heptactis*. Six other species have been found, however, although very rarely, including *A. arachnae* (Bréb.) Ralfs, *A. elegans* Grev., *A. hookeri* Ehrenberg, *A. robustus* Castr., *A. roperianus* (Grev.) Ralfs and *A. shadboltianus* Castr. Some of these have been reported as fossils only, while others as both fossil and living.

This is the first report of the occurrence of *Asteromphalus sarcophagus* Wallich in Chile. The species was found only in northern waters. Great variability of valve shape found in this species led us to synonymize the forms *obovatus* and *pandorae* described by Thorrington-Smith, as well as *A. hustedtii* (Kolbe) Thorrington-Smith and *A. petterssonii* (Kolbe) Thorrington-Smith, with *A. sarcophagus*.

The structure of the cingulum of *A. heptactis* is described. This is the first time the distal end of the hyaline rays of this species is shown to be occluded by a thin layer of silica with a small central perforation. The external opening of the labiate process is at the basal end of the ray. Previous observations suggest presence of the occluding layer in other genera of the Asterolampraceae as well.

Using data from the literature, a key for the differentiation of all species of *Asteromphalus* reported from the Chilean coast is given.

Introduction

The family Asterolampraceae H. L. Smith is comprised, according to Gombos (1980), of the following genera: *Asterolampra* Ehrenberg, *Asteromphalus* Ehrenberg, *Bergonia* Tempère, *Rylandsia* Greville, and *Discodiscus* Gombos. Simonsen (1972, 1979) also included *Brightwellia* Ralfs in the family. However, Ross and Sims (1973) and Gombos (1980) did not agree with Simonsen's suggestion. Ross and Sims proposed that *Brightwellia* be placed within the Coscinodiscaceae, while Gombos considered it an independent branch of the Coscinodiscaceae and not in the main developmental line leading to the

Asterolampraceae. Presently the members of the Asterolampraceae are defined by partially areolated valve surfaces, marginal labiate processes, and hyaline rays opened to the interior of the valve through ray-slits and to the exterior through holes at the marginal ends.

Asterolampra and *Asteromphalus* are the only members of the Asterolampraceae present in modern oceans. *Asteromphalus*, with seven species, is the only genus reported either from fossil deposits or recent samples along the Chilean coast, and the species include *A. arachne* (Bréb.) Ralfs, *A. elegans* Greville, *A. hookeri* Ehrenberg, *A. robustus* Castracane, A. *roperianus* (Grev.) Ralfs, *A. shadboltianus* (Grev.) Ralfs, and *A. heptactis* (Bréb.) Ralfs (Rivera 1983; Rivera et al. 1990).

Asteromphalus differs from the other genera of the family principally by having one hyaline ray narrower, conferring to the valve a bilateral symmetry. Although *A. heptactis* is the most common species of the genus reported from both coastal and oceanic waters along the Chilean coast, it is always scanty, except in some samples collected south of 40.S. In spite of the fact that this species has been studied with electron microscopy by several workers in the last 15 years (Okuno 1951, 1964; Fryxell and Hasle 1973; Gerloff and Helmcke 1974; Takano 1983; Ricard 1987; and others), some of its morphological features, among them the structure of the cingulum, are still practically unknown. In general, these studies have been done on only a few frustules. Because of this, it has not been possible to compose a complete image of its morphological variability. Some of the features are likely to exhibit a wide range of variation, even within the same species (number of hyaline rays, position of the central area, etc.).

Continuing our attempt to enhance the knowledge of the morphology and taxonomy of the marine diatom flora off the Chilean coast, and with the specific intention of making a study on the species of the genus *Asteromphalus*, a considerable number of samples deposited at the Diatom Collection of the University of Concepción, Chile, was reviewed.

Materials and Methods

Samples studied were collected along the Chilean coast between 18.20'S and 45.52'S. Material from the Indian Ocean was collected during the A. Bruun Expedition in 1963 and was made available to us by Prof. J. Gerloff (Botanisches Institut Berlin Dahlem). All samples are deposited in the Diatom Collection, Department of Botany, Universidad de Concepcion, Chile. (DIAT-CONC). Samples for both light and electron microscopy studies were treated for removal of organic matter according to the method described by Hasle and Fryxell (1970). A Zeiss Photomicroscope III was used for light microscopy. For electron microscopy, cells were dried following the method of Anderson (1951). Electron microscopy studies were made at the Laboratory of Electron Microscopy, Universidad de Concepcion. Photographs were taken on an ETEC Austoscan U-1 scanning electron microscope, and transmission electron micrographs were taken by means of a Philips EM 200. The terminology used for the Asterolampraceae is that suggested by Anonymous (1975), Ross et al. (1979), and by Gombos (1980), in particular.

Observations

Asteromphalus sarcophagus Wallich
(Figs. 1–30)

Wallich 1860:47, Pl. 2, Fig. 12. Rattray 1890:666. De Toni 1894:1, 417.
SYNONYMS: *Asteromphalus sarcophagus* f. *obovatus* Thorrington-Smith 1970:821, Pl. 1, Fig. 3. *Asteromphalus sarcophagus* f. *pandorae* Thorrington-Smith 1970:821, Pl. 1, Fig. 2. *Asteromphalus hustedtii* (Kolbe) Thorrington-Smith 1970:822, Pl. 1, Fig. 4 (*Liriogramma hustedtii*

Kolbe 1955:173, Fig. 6; Pl. 2, Fig. 21). *Asteromphalus petterssonii* (Kolbe) Thorrington-Smith 1970:822, Pl. 1, Fig. 5 (*Liriogramma petterssonii* Kolbe 1954:40, Fig. 9; Pl. 4, Figs. 46a, b).

MATERIALS: Pacific Ocean: DIAT-CONC 2186, MarChile VIII, St. 12, 25.08. 1972, 18.20'S, 74.16'W. DIAT-CONC 3900, MarChile VIII, St. 12, 08.08.1972, 18.20'S, 74.16'W. Indian Ocean: DIAT-CONC 1668, A. Bruun, N. 143, 1963, 01.54'S, 79.52'E.

AMENDED DIAGNOSIS: Valves flat, 18–111 µm length, 9–23 µm width, oblong or linear-oblong through ovoid to ovoid-lanceolate, usually more or less constricted near one (Figs. 2–5, 16, 23–26) or both rounded extremities, giving the valve, in the latter cases, a sarcophagus-like shape (Figs. 1, 10–15). Central hyaline area, formed by the central expansion of the rays, about one half the length of the transapical axis and located centrally (Figs. 9, 28–30) to markedly eccentric (Figs. 1–5, 10–20, 24–27), with separating lines smooth (Figs. 1–3). Five broad hyaline rays, symmetrically located on the valve, appear elevated on the external valve surface (Fig. 4). Coinciding with the apical axis, a broad hyaline ray is always found opposite a sixth narrower hyaline ray. Depending on the shape of the valve and on the position of the central area, all of the broad hyaline rays are either of approximately the same or different length. All the rays extend only to near the edge of the valve and thus appear to have rounded ends (Fig. 6). The rays open to the exterior through a hole located at the marginal end and to the interior by a linear to undulate ray-slit (Figs. 3, 5). At internal marginal ends the rays have a well-differentiated labiate process. The labiate processes lack external tubes but their simple circular opening can be recognized from the outside at the basal side of the ray-hole (Fig. 6). Internally, the labiate processes are stalked and each longitudinal slit, surrounded by two lips, is curved (Fig. 7), particularly in the case of the narrow hyaline ray (Fig. 8). Areolae usually form radial striae but varying to distorted or irregular apical rows in different specimens, 6–11 in 10 µm near the apical axis (inner margin of the areolated segment) and smaller toward the valve margin, 11–12 in 10 µm (Figs. 1–5). Areolae are subcircular in outline, with internal foramen and external cribra with circular to elongated uniformly distributed pores, about 4–5 in 1 µm (Figs. 6, 8). This diagnosis is based on the descriptions of *A. sarcophagus*, *A. sarcophagus* f. *pandorae*, *A. sarcophagus* f. *obovatus*, *Liriogramma hustedtii*, *L. petterssonii,* and on our own material from the Pacific and Indian oceans.

Data from literature reveals that *Asteromphalus sarcophagus*, including the taxa we consider as synonyms, have always been found in tropical and subtropical zones. The taxon is known for the Atlantic Ocean between the Gulf of Mexico and 07.8'S (Kolbe 1955; Thorrington-Smith 1970), for the Indian Ocean between 10.N and 25.09'S (Wallich 1860; Heiden and Kolbe 1928; Kolbe 1956; Taylor 1966; Thorrington-Smith 1970; Simonsen 1974), and for the Pacific Ocean. In the Pacific Ocean the furthest north (6.44'N–129.28'W) and the furthest south (2.52'S–89.50'W) locations have been recorded by Kolbe (1955) as *Liriogramma hustedtii* and *L. petterssonii* (Kolbe 1954) respectively. However, our samples reveal presence of *A. sarcophagus* as far as 18.20'S–74.16'W. The species was found infrequently very scanty and only in two vertical plankton samples in the same locality. Frustules of *A. sarcophagus* appear to be extremely fragile, and many of the specimens observed were found eroded or only as fragments.

External cribrum of areolae is convex and slightly raised above the valve surface, with regularly distributed pores. The shape of areolae is relatively constant, and basically there were no differences in the number of areolae in the material studied when compared with data from literature or from measurements made on illustrations available (Table 1).

Thorrington-Smith (1970) has emphasized that one of the principal differences between *A. hustedtii* or *A. petterssonii* and *A. sarcophagus* is the presence of puncta in the former

TABLE I. Morphologic data on *Asteromphalus sarcophagus* from the literature and from the present study.

	Wallich 1860	Kolbe 1954	Kolbe 1955	Thorrington-Smith 1970			Simonsen 1974		Present study
		as *Lirogramma petterssonii*	as *Lirogramma hustedtii*	as *Asteromphalus hustedtii*	as *Asteromphalus sarcophagus* f. *sarcophagus*	as *Asteromphalus sarcophagus* f. *obovatus*	as *Asteromphalus sarcophagus* f. *pandora*		
Apical axis (µm)	45.7 (0.0018")	56	24–26	30	20–32 (60)	30	86–111	20.5–35*	22–38
Transapical axis (µm)	22 (0.0009")	16	1–12	10	16–22	12	16–17	17.2–22.3*	9–18
Areolae – inner margin	–	?	?	?	6–7*	?	7*	7–8*	8–11
Areolae –	–		10	10		6–10	10	6	– –
Areolae – valve margin	–	?	?	?	8–9*	?	8–9*	9–10*	11–12
Orientation of areolae	–	apical and transapical rows of punctae	radial to distorted*	irregular; without areolae	radial*	radial*	radial and distorted	radial*	radial to distorted
Shape of valves	oblong with slight constriction near each extremity; pyriform	lanceolate to ovoid	oviform	oviform	rhombic with concave sides, rounded extremities	obovate	linear-oblong	rhombic with concave sides, rounded extremities*	rhombic with concave sides (rounded extremities) to oblong with variable constricted ends

TABLE 1. continued.

	Wallich 1860	Kolbe 1954	Kolbe 1955	Thorrington-Smith 1970			Simonsen 1974	Present study
		as *Liriogramma petterssonii*	as *Liriogramma hustedtii*	as *Asteromphalus hustedtii*	as *Asteromphalus sarcophagus* f. *sarcophagus*	as *Asteromphalus sarcophagus* f. *obovatus*	as *Asteromphalus sarcophagus* f. *pandora*	
Number hyaline rays	6	6	6	6	6	6	6	6	6
Location of central area	eccentric	centric	eccentric*	eccentric	centric to markedly eccentric	eccentric	slightly eccentric	eccentric to markedly eccentric*	eccentric to markedly eccentric
Labiate processes	–	–	–	–	marginal spine at end of each broad hyaline ray; narrow hyaline ray terminates in a large areola	marginal spine at end of each broad hyaline ray; narrow hyaline ray terminates in a large areola	marginal spine at end of each hyaline ray; narrow hyaline ray terminates in a large areola	–	one at each marginal end of hyaline rays
Distribution	Indian Ocean	South Pacific Ocean	North and South Atlantic and Pacific Oceans	South Atlantic Ocean	North and South Indian Ocean	North and South Indian Ocean	South Indian Ocean	South Indian Ocean	South Pacific and South Indian Oceans

*Information obtained from illustration

species and areolae in the latter. In the Chilean material only one *A. hustedtii*-like valve was found (Fig. 18), and because of this, it was impossible to prepare it for SEM. The general appearance of the individual corresponds to typical *A. sarcophagus* cells. The perforations appear brighter, however, and this may be due to a higher content of silica or simply that one is dealing with an anomalous cell. It should be mentioned that Kolbe (1955) in his description of *Liriogramma hustedtii* Kolbe referred to these perforations specifically as "areolae."

In the Chilean material the length/breadth ratio of the cells varies from 1:2.2 to 1:3. Great variability in the degree of concavity of the sides at each end of the valve was observed. This range of variation is shown in Figures 9–30 and represents a continuum of forms from one extreme to the other. This, together with the fact that no real differences exist in relation to the number of hyaline rays and areolae, and that all these forms share the same geographical distribution, has led us to consider all forms previously described as different taxa, as synonyms of *A. sarcophagus*. We include *Asterophalus hustedtii* (Kolbe) Thorrington-Smith and *A. petterssonii* (Kolbe) Thorrington-Smith as synonyms of *A. sarcophagus*. The occurrence of "central markings" and of "irregular areolation" observed by Kolbe in both taxa were considered by him as primitive characters and were the basis for his creation of the new genus *Liriogramma*. Based on our observations we cannot detect fundamental differences in the morphology of *A. hustedtii*, *A. petterssonii*, and *A. sarcophagus*. Furthermore, in some of our specimens an undulated narrow hyaline ray, similar to that illustrated by Kolbe for his *L. petterssonii* and by Thorrington-Smith (1970) for his form *pandorae*, can be discerned (Figs. 2, 3, 5, 25). Finally, we are in agreement with Simonsen (1974) in the sense that *Liriogramma* species are "malformations of some sort."

Asteromphalus heptactis (Brébisson) Ralfs
(Figs. 31–42)

Ralfs in Pritchard 1861:838, Pl. 8, Fig. 21. Okuno 1964:23, Pl. 443. Takano 1983, sheet 128.

BASIONYM: *Spatangidium heptactis* Brébisson 1857:296, Pl. 3, Fig. 2.

SYNONYMS: *Asteromphalus reticulatus* Cleve 1873:5, Pl. 1, Fig. 2. *Asteromphalus ralfsianus* (Norman) Grunow in Schmidt et. al. 1876, Pl. 38, Figs. 6, 7. *Asteromphalus ornithopus* Karsten 1905:90, Pl. 8, Fig. 13.

MATERIALS: Pacific Ocean: DIAT-CONC 3901, MarChile VIII, St. 12, 18.20'S–74.16'W, 08.08.1972. DIAT-CONC 3634, MarChile VIII, St. 13, 18.96'S–74.47'W, 19.08.1972. DIAT-CONC M-1287, Exp. Downwind, St. 29, 22.38'S–72.00'W, 02.01.1958. DIAT-CONC M-2165, Bahia Concepción, 36.43'S–73.00'W, 14.06.1965. DIAT-CONC M-2169, Bahía Concepción, 36.43'S–73.05'W, 09.06.1965. DIAT-CONC M-1356, 38.00'S–73.50'W, 22.11.1978. DIAT-CONC 2282, 40.40'S–74.07'W, 15.11.1970. DIAT-CONC M-1260, 41.48'S–73.05'W, 29.04.1977. DIAT-CONC 2555, 41.49'S–73.05'W, 05.08.1977. DIAT-CONC 2575, 41.49'S–73.05'W, 08.10.1977. DIAT-CONC 2360, 45.12'S–75.28'W, 16.11.1978. DIAT-CONC 2286, 45.52'S–75.40'W, 16.11.1970.

Cells are single, in girdle view rectangular to drum-shaped with slightly convex and radially undulated valves (Fig. 31). Pervalvar axis 14–30 µm. One broad and homogeneously silicified band in each cingulum, 5.6–7.3 µm width (Figs. 31, 32). Valves subcircular to oval, 29–50 µm in diameter. Central hyaline area circular to polygonal, eccentric, about 1/3 the diameter of the cell; separating lines jagged (Figs. 33, 34). Six to seven broad hyaline rays (2.8–4 µm width), plus a narrow one, are elevated on the external valve

surface and extend to edge of valve. The rays appear square-ended externally, but with rounded ends in internal valve view (Figs. 35, 36). Narrow hyaline ray (0.9–1.5 µm width) is usually slightly longer and only somewhat raised. If six broad hyaline rays are present, three of them are arranged on one side of the valve and the others on the opposite side (separated by the narrow hyaline ray; Figs. 34, 35); when seven broad hyaline rays are present they retain the same position and the additional ray follows in line with the narrow hyaline ray (Fig. 33). Each hyaline ray opens inward by a somewhat linear ray-slit (Figs. 35, 36). At the marginal external end the ray is occluded by a slightly depressed and delicate layer of silica, oriented perpendicular to the valvar plane (Figs. 32, 37–41). This layer has a central, circular hole of ca. 0.2–0.4 µm in diameter, bordered by one or two hyaline rings of silica (Figs. 37–39). These rings usually appeared eroded. In the basal part of the distal end of the hyaline rays there is a second hole, of approximately the same diameter, which corresponds to the external opening of the labiate process (Figs. 37–40).

Although broad and narrow hyaline rays are similar in these structural features, they differ in other aspects of their structure. The broad hyaline rays have an external marginal end section that is circular in shape (ca. 1.9–2.5 µm in diameter), with its basal portion formed by two linear segments arranged at approximately 90 degrees (Figs. 37–39). The narrow hyaline ray, however, has an elongated (Fig. 42), or sometimes horseshoe-shaped external marginal end section with its internal basal and lateral sides with areolae-like perforations (Fig. 41). The internal part of each labiate process is well differentiated and the slit is curved. Areolated segments taper towards the center of the valve. Areolae are somewhat hexagonal, 6–8 in 10 µm, usually uniform in size and only slightly smaller in the valve margin, forming lines parallel to the marginal prolongation of the hyaline rays as well as tangential lines (Figs. 33–35). External cribra have subcircular pores uniformly distributed, 4–5 in 1 µm, and circular to subcircular internal foramen, 1.2–1.5 µm in diameter. Areolae are connected by passage pores (Fig. 36).

Asteromphalus heptactis, the most common species of the genus, is a cosmopolitan plankton taxon. Simonsen (1974) pointed out some reservations about its designation as oceanic as proposed by Cupp (1943), Hendey (1964), and Sournia (1968). Material studied in this paper was collected along the Chilean coast between 18.20'S and 45.52'S, and the species was particularly abundant in coastal samples south of 40.S. The species had been previously reported for the Chilean coast between 20.39'S and 51.35'S (Krasske 1939, 1941; Balech 1962; Rivera 1969; Fenner et al. 1976; Uribe et al. 1982). Okuno (1951, 1964), Fryxell and Hasle (1973), Gerloff and Helmcke (1974), and Ricard (1987) have previously studied the species by electron microscopy. Morphological data of *A. heptactis* compiled both from the literature and from the Chilean material examined in this paper are summarized in Table 2.

Asteromphalus heptactis is very closely related to *A. parvulus* Karsten (1905:90, Pl. 8, Fig. 14). Priddle and Fryxell (1985) found it impossible to distinguish between the two in routine analysis of samples. However, *A. parvulus* has a larger central area (about one half the valve diameter) located symmetrically on the valve, usually fewer broad hyaline rays, smaller areolae, and has been found mostly in subantarctic and antarctic waters. The individual shown by Fenner et al. (1976, Pl. 4, Fig. 2) as *Asteromphalus hookeri* Ehrenberg has an oval valve, jagged separating lines, and a markedly eccentric central area, and these features would assign it to *A. heptactis*.

The following key has been developed from our observations as well as from data in the literature, to separate the eight taxa of *Asteromphalus* reported so far from Chilean samples.

The characteristics used are discernible by light microscopy.

1 Valves elongated, rhombic with concave to oblong sides with variably constricted round ends . . . . . *A. sarcophagus*
1' Valves circular to suboval 2
2 Central area located symmetrically on the valve 3
2' Central area eccentric 5
3 Separating lines smooth, sometimes bifurcated. Marginal external end of broad hyaline rays round-ended . . . . . *A. hookeri*
3' Separating lines jagged. Marginal external end of broad hyaline rays square-ended 4
4 Areolae 5–8 in 10 µm. Valve diameter usually < 60 µm . *A. heptactis*
4' Areolae 12–16 in 10 µm. Valve diameter usually 80 µm . *A. roperiatus*
5 Central area small ca. 1/6–1/7 the valve diameter and markedly eccentric. Usually 4 broad hyaline rays with rounded marginal external ends . . . *A. arachne*
5' Central area about 1/4–1/2 the valve diameter 6
6 Areolae 5–8 in 10 µm. Five to seven broad hyaline rays with square external marginal ends . . . . . *A. heptactis*
6' Areolae usually more than 10 in 10 µm 7
7 Ten to twelve broad hyaline rays. Valves circular. Central area about 1/3 with respect to the valve diameter . . . . . *A. elegans*
7' Four to eight broad hyaline rays 8
8 Valves 25–50 µm in diameter. Areolae 12 in 10 µm . . . *A. robustus*
8' Valves larger. Areolae up to 14 in 10 µm . . . . . *A. shadboltianus*

Asteromphalus arachne (Bréb.) Ralfs was reported from Arica (ca. 18.28'S–70.20'W) by Schmidt 1886 in Schmidt et al. (1874– 1959). *Asteromphalus elegans* Greville was observed in material from Mejillones (ca. 23.06'S–70.27'W) by Boyer (Rivera and Gebauer 1989) and off Antofagasta (ca. 20.30'S–69.00'W) by Hendey (1937). Belyaeva (1972) reported this taxon from the South Pacific Ocean between O.S. and 32.S. *Asteromphalus hookeri* Ehrenberg was found off the coast of Mejillones by Hendey (1937) and in the Strait of Drake (ca. 58.54'S–66.08'W) by Meyer (1966). *Asteromphalus robustus* Castracane was reported from Tripoli of Tiltil (ca. 33.05'S–70.56'W) and Tripoli of Mejillones (ca. 23.06'S–70.27'W) by Frenguelli (1949), and also from Mejillones by Tempère and Peragallo (1907) as *A. brookei* Grunow. *Asteromphalus roperianus* (Grev.) Ralfs was found in Tripoli of Mejillones (ca. 23.06'S–70.27'W) by Rattray (1890), and by Tempère and Peragallo (1907), and by Frenguelli (1949). *Asteromphalus shadboltianus* (Grev.) Ralfs has been reported only from Tripoli of Mejillones (Rattray 1890; Möller 1891; Tempère and Peragallo 1907; Frenguelli 1949).

Discussion

A salient feature of these results is the great variation in the morphology of the species under study. It appears that this situation is likely to be encountered in all members of the genus *Asteromphalus*, as well as in those belonging to *Asterolampra*, following Simonsen (1974).

The main criteria for distinguishing among species of *Asteromphalus* traditionally have been the number of broad hyaline rays, size, and position of the central area on the valve face and the number of areolae. Recognizing that these characteristics, as well as others found in the present study, exhibit a wide range of variation within a taxon, we agree with Simonsen (1972) in the sense that one has to make use of them with the utmost

TABLE 2. Morphologic data on *Asteromphalus heptactis* from the literature and from the present study.

	Shape of valves	Valve diameter	Total number of hyaline rays	Position of central area	Ratio of central area to valve diameter	Areolae number	Number of perforations in cribrum (in 1 µm)	Number of bands per cingulum	Width of each band
Hustedt 1930	circular to oval	42 – 175	7	eccentric	1/4	5 – 7	–	–	–
Hendey 1937	discoid to oval	64 – 110	7	eccentric	1/4 – 1/3	–	–	–	–
Cupp 1943	subcircular*	38 – 100	7	slightly eccentric	1/4 – 1/3	6 – 6.5	–	–	–
Hendey 1964	discoid	50 – 100	7	centric ?	1/4 – 1/3	–	–		
Okuno 1951	subcircular	30 – 90	6 – 7	eccentric	1/4 – 1/3	6 – 7	3 – 4		
Okuno 1964	subcircular	ca. 70	4 – 7	eccentric	1/4 – 1/3	6 – 7	4	–	–
Fryxell & Hasle 1973	subcircular to oval*	–	7*	eccentric*	–	–	–	–	
Fenner et al. 1976	circular to oval	31 – 45	7*	eccentric	1/3	6 – 7	–	–	–
Takano 1983	subcircular*	38 – 100	7*	eccentric*	1/4 – 1/3	5 – 7	–		–
Priddle & Fryxell 1985	circular*	30 – 55	6 – 7	centric	large	–	–		–
Ricard 1987	subcircular to oval*	–	7*	eccentric*	1/4 – 1/3*	–	–		
Present study	subcircular to oval	29 – 50	7 – 8	eccentric	1/3	6 – 8	4 – 5	1	5.6 – 7.3

* information obtained from illustration

discrimination and, following Priddle and Fryxell (1985), not singly but in conjunction with other relevant features.

Asteromphalus sarcophagus serves as an excellent example to illustrate variation of the general outline of the valves. Although in this species the elongated shape of the valves differs considerably with the generalized circular outline in the other members of the genus, the range of variation observed in the Chilean material allowed us to synonymize the forms *obovatus* and *pandorae* described by Thorrington-Smith (1970) with the species of Wallich, as we also did with *A. hustedtii* and *A. petterssonii*. In *A. heptactis*, variation in valve shape is not as notorious, and is usually reported as subcircular to oval, except by Hendey (1964) and by Priddle and Fryxell (1985), who described it as discoid or circular, respectively. We consider the systematic value of this characteristic of little importance.

The position of the central area in *Asteromphalus sarcophagus* was observed to be also highly variable, from centric to markedly eccentric. In *A. heptactis*, however, it always retains an eccentric position, as reported in the majority of previous studies. A similar situation is found regarding the number of broad hyaline rays, which is constant in *A. sarcophagus* and quite variable in *A. heptactis*. In both taxa length of the hyaline rays varies depending on the shape of the valve, and this is particularly so in the case of *A. sarcophagus*, as shown in the present study. In summary, characterization of *Asteromphalus* taxa should be attempted only after a fairly large number of individuals have been examined.

As far as we know, the structure of the girdle in the genus *Asteromphalus* has not been observed or described previously by means of electron microscopy. This assumption seems also to be valid for the rest of the members of the family Asterolampraceae, as no references are made to it in recent papers (Okuno 1964; Fenner et al. 1976; Takano 1983; Gombos 1980; Ricard 1987). Only single valves were found of *A. sarcophagus*, and thus the structure of its cingulum is still unknown. The cingulum has been observed only in *A. heptactis*. In this species, the characteristics of these hyaline bands were very constant in all individuals observed. These bands are completely different from those in *Rylandsia biradiata* (Gombos 1980, Fig. 56), where vertical lines of perforations are distinct. Perhaps after a thorough and detailed examination of the structure of the cingulum in the Asterolampraceae, its characteristics could be used as additional criteria to distinguish between the various genera or species, as done in other centric diatoms, e.g., in the genus *Thalassiosira* (Fryxell et al. 1981).

One of the most interesting findings of this study was the recognition, in *Asteromphalus heptactis*, of a thin wall of silica with a small central opening, occluding the external marginal end of both broad and narrow hyaline rays. Previous information about the Asterolampraceae described the hyaline rays as opening to the exterior through a large hole positioned at their marginal ends (Fryxell and Hasle 1973; Ross and Sims 1973; Gombos 1980). Although Fryxell and Hasle (1973), as well as Ricard (1987), referred to this opening as a "pseudonodule," such a designation was considered erroneous by Simonsen (1975) and by Gombos (1980), who simply used the words "hole" and "ray hole," respectively. In all samples prepared for SEM by critical point drying, presence of the silica layer could be recognized. However, when samples were treated to remove the organic matter, the silica layer did not stand up to this processing; after treatment the ends of the hyaline rays appear simply as large holes.

Although this is the first time that this peculiar structure is described for the genus *Asteromphalus*, it should be pointed out that it can be recognized in figures obtained by other

authors. Gombos (1980, Fig. 46), in a marginal view of *Asterolampra marginata* aff. var. *curvilineata* Brun, shows two hyaline rays where their external holes appear occluded by a membrane. This same layer can also be clearly discerned in his Figure 49, corresponding to *Discodiscus tetraporus* (Brun) Gombos. Similarly, the silica layer is also recognizable in *Asteromphalus heptactis*, as presented by Takano (1983) in his Figure B of sheet 128. However, in none of these figures is it possible to detect either the presence of the central perforation or that corresponding to the labiate process. Considering these points, it seems plausible to assume that the presence of this layer is a characteristic feature of the Asterolampraceae. The general appearance of this layer, with the exception of a closely positioned labiate process, is very similar to the operculate pseudonodule described for *Actinocyclus circellus* Watkins by Watkins and Fryxell (1986). It should be recalled, however, that pseudonodules, typical of the family Hemidiscaceae, are known to occur only one per valve, and this is not the case in *Asteromphalus*.

It is expected that research now in progress, using the critical point drying method, will contribute additional information about the relevance of the silica layer as a distinctive feature of the Asterolampraceae.

Literature Cited

ANDERSON, T. F. 1951. Techniques for the preservation of three dimensional structure in preparing specimens for the electron microscope. Trans. N. Y. Acad. Sci. II, 13:130–134.

ANONYMOUS. 1975. Proposals for a standardization of diatom terminology and diagnosis. Nova Hedwigia, Beih. 53:323–354.

BALECH, E. 1962. Tintinoidea y Dinoflagellata del Pacífico según material de las expediciones Norpac y Downwind del Instituto Scripps de Oceanografía. Revista del Instituto de Investigaciones de Ciencias Naturales, Buenos Aires, Zoología 7:1–253.

BELYAEVA, T. V. (1972). Distribution of large diatom algae in the Southeastern Pacific. Okeanologiya 12:475–483.

BRÉBISSON, A. de. 1857. Refermant la description de quelques nouvelles Diatomees observées dans le Guano de Pérou, et formant le genre *Spatangidium*. Bull. Soc. Linnéenne de Normandie 2:292–298.

CLEVE, P. T. 1873. On diatoms from the Arctic Sea. Bihang Kongl. Svenska Akad. Handl. 1:1–28.

CUPP, E. E. 1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Ocean. 5:1–238.

DE TONI, J. B. 1891–1894. Sylloge algarum omnium hucusque cognitarum, vol. II, Bacillarieae; sectio I, Raphideae, pp. 1–490 (1891); sectio II, Pseudoraphideae, pp. 491–817 (1892); sectio III, Cryptoraphideae, pp. 818–1556 (1894). Typis Seminarii, Patavii.

FENNER, J., H. J. SCHRADER, AND H. WIENICK. 1976. III. Diatom phytoplankton studies in the southern Pacific Ocean, composition and correlation to the Antarctic convergence and its paleoecological significance. Initial Reports of the Deep Sea Drilling Project 35:757–813.

FRENGUELLI, J. 1949. Diatomeas fósiles de los yacimientos chilenos de Tiltil y Mejillones. Darwiniana 9:97–157.

FRYXELL, G. A. AND G. R. HASLE. 1973. Coscinodiscineae: Some consistent patterns in diatom morphology. Nova Hedwigia, Beih. 45:69–96.

FRYXELL, G. A. G. F. HUBBARD, AND T. A. VILLAREAL. 1981. The genus *Thalassiosira*: variations of the cingulum. Bacillaria 4:41–63.

GERLOFF, J. AND J-G. HELMCKE. 1974. Tafel 715–824 *in* Diatomeenschalen im elecktronenmikroskopischen Bild. Teil VIII. J-G. Helmcke, W. Krieger and J. Gerloff, eds. J. Cramer, Lehre.

GOMBOS, Jr., A. M. 1980. The early history of the diatom family Asterolampraceae. Bacillaria 3:227–272.

HASLE, G. R. AND G. A. FRYXELL. 1970. Diatoms: cleaning and mounting for light and electron microscopy. Trans. Amer. Microsc. Soc. 89:469–474.

HEIDEN, H. AND R. W. KOLBE. 1928. Die marinen Diatomeen der deutschen Sud-Polar Expedition 1901–1903. Deut. Sud-Polar Exp. 8:450–714.

HENDEY, N. I. 1937. The plankton diatoms of the Southern Seas. Discovery Rep. 16:151–364.

———. 1964. An introductory account of the smaller algae of British coastal waters. Part V: Bacillariophyceae (Diatoms). Her Majesty's Stationery Office, London, 317 pp.

HUSTEDT, F. 1930. Die Kieselalgen *in* Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz, L. Rabenhorst, ed. 7:1–920.

KARSTEN, G. 1905. Das Phytoplankton des Antarktische Meeres nach dem Material der deutschen Tiefsee-Expedition 1898–1899, in Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898–1899, C. M. Chen, ed. 2:3–136.

KOLBE, R. W. 1954. Diatoms from equatorial Pacific cores. Rep. Swedish Deep-Sea Exp. 1947–1948, 6:1–49.

———. 1955. Diatoms from equatorial Atlantic cores. Rep. Swedish Deep-Sea Exp. 1947–1948, 7:151–184.

———. 1956. Diatoms from equatorial Indian Ocean cores. Rept. Swedish Deep-Sea Exp. 1947–1948, 9:1–50.

KRASSKE, G. 1939. Zur Kieselalgenflora Südchiles. Arch. Hydrobiol. 35:349–468.

———. 1941. Die Kieselalgen des chilenischen Küstenplanktons. Arch. Hydrobiol. 38:260–287.

MEYER, R. 1966. Contribución al estudio del fitoplancton del Paso de Drake. Cuaderno 1, Ciencias del Mar, Universidad Católica de Valparaiso 41–82.

MÖLLER, J. D. 1891. Lichtdrucktafeln hervorragen scüner und vollständiger Müller'scher Diatomaceen-Praparate, 1891, Verzeichniss der in den Lichtdrucktafeln Möllerscher Diatomaceen-Präparate enthaltenen Arten. Wedel.

OKUNO, H. 1951. Electron microscopical study on antarctic diatoms. J. Jap. Bot. 26:305–310.

———. 1964. Fossil diatoms. Pl. 414–513 *in* Diatomeenschalen im elektronenmikroskopischen Bild, Teil V. J-G. Helmcke and W. Krieger, eds. J. Cramer, Lehre.

PRIDDLE, J. AND G. FRYXELL. 1985. Handbook of the common plankton diatoms of the southern ocean. Centrales except the Genus *Thalassiosira*. British Antarctic Survey, Cambridge. 159 pp.

PRITCHARD, A. 1861. A history of the infusoria, including the Desmidiaceae and Diatomaceae, British and foreign. Whittaker and Co., London. 968 pp.

RATTRAY, J. 1890. A revision of the genus *Coscinodiscus* Ehrenberg and some allied Genera. Proc. R. Soc. Edinburgh, 24:449–692.g

RICARD, M. 1987. Diatomophycees. *In* Atlas du Phytoplancton Marin, Vol. 2. A. Sournia, ed. Centre National de la Recherche Scientifique, Paris. 297 pp.

RIVERA, P. 1969. Sinopsis de las Diatomeas de la Bahía de Concepción, Chile. Gayana, Bot. 18:1–112.

———. 1983. A guide for references and distribution for the class Bacillariophyceae in Chile between 18.28'S and 58.S. Bibl. Diatomologica 3:1–386.

RIVERA, P. AND M. GEBAUER. 1989. Diatomeas chilenas en las Colecciones de Boyer, Cleve and Möller, Schulze y Smith, depositadas en la Academia de Ciencias Naturales de Filadelfia, Estados Unidos. Gayana, Bot. 46:89–116.

RIVERA, P., M. GEBAUER, AND H. BARRALES. 1990. A guide for references and distribution for the class Bacillariophyceae in Chile between 18.28'S and 58.S. Part II. Data from 1982 to 1988. Gayana, Bot. 46:155–198.

ROSS, R. AND P. A. SIMS. 1973. Observations on family and generic limits in the Centrales. Nova Hedwigia, Beih. 45:97– 130.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

SCHMIDT, A. 1874–1959. Atlas der Diatomaceen-Kunde. R. Reisland, Leipzig. Taf. 1–472.

SIMONSEN, R. 1972. Ideas for a more natural system of the centric diatoms. Nova Hedwigia, Beih. 39:37–54.

———. 1974. The diatom plankton of the Indian Ocean Expedition of R/V "Meteor" 1964–65. "Meteor" Forschungsergebnisse, ser. D, 19:1–107.

———. 1975. On the pseudonodulus of the centric diatoms, of Hemidiscaceae reconsidered. Nova Hedwigia, Beih. 53:83–94.

———. 1979. The diatom system: ideas on phylogeny. Bacillaria 2:9–71.

SOURNIA, A. 1968. Diatomees planctoniques du Canal de Mozambique et de L'Ile Maurice. Memoire Office de Recherche Scientifique et Technique Outre-Mer 31:120.

TAKANO, H. 1983. Sinopsis of red-tide organisms. Working Party on Taxonomy in the Akashiwo Kenkyukai, ed. Fisheries Agency, Japanese Government, Sheet 128.

TAYLOR, F. J. R. 1966. Phytoplankton of the south west Indian Ocean. Nova Hedwigia 12:433–766.

TEMPÈRE, J. AND H. PERAGALLO. 1907. Diatomées du Monde Entier. Ed. 2, Arcachon, Grez-sur-Loing (S.-et -M.) 1:1–16.

THORRINGTON-SMITH, M. 1970. Some new and little-known planktonic diatoms from the west Indian Ocean. Nova Hedwigia, Beih. 31:815–835.

URIBE, E., S. NESHYBA, AND T. FONSECA. 1982. Phytoplankton community composition across the west wind drift off South America. Deep-Sea Res. 29:1229–1243.

WALLICH, G. C. 1860. The siliceous organisms found in the digestive cavities of the Salpae, and their relation to the flint nodules of the chalk formation. Trans. Microsc. Soc. N. S. 8:36–55.

WATKINS, T. P. AND G. A. FRYXELL. 1986. Generic characterization of *Actinocylus*: consideration in light of three new species. Diatom Res. 1:291–312.

Explanation of Plates

Plate 1, Figures 1–8

FIGURES 1–8. *Asteromphalus sarcophagus*. FIGURES 1–2. LM. Areolae usually forming radial striae, but distorted or irregular rows may be present. Number of broad hyaline rays (5) very constant in the species. FIGURES 3, 5. SEM. Internal valve views. Rays open to the interior by a linear to undulate ray slit. FIGURE. 4. SEM. Hyaline rays appear elevated on external valve surface. FIGURE 6. SEM. All rays extend only to near edge of valve and open to exterior through a hole located at marginal end. FIGURES 7–8. SEM. Internal view of labiate processes, located at the marginal end of hyaline rays; longitudinal slit curved, particularly in the case of the narrow hyaline ray (Fig. 8).

Plate 2, Figures 9–30

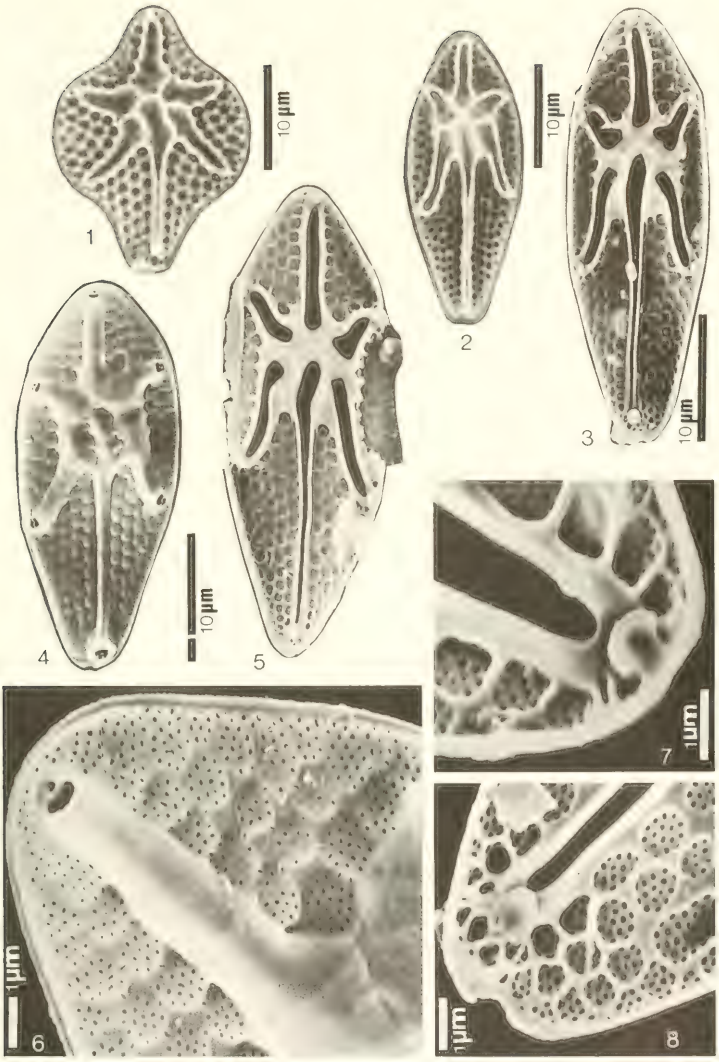
FIGURES 9–30. Range of cell variability in *Asteromphalus sarcophagus* and in allied taxa. Figures 9–10 according to Thorrington-Smith 1970; Figures 11–12, 14–15 according to Simonsen 1974; Figures 13, 16–18, 22–26 present study. FIGURES 19–20. *Liriogramma hustedtii*. FIGURE 21. *Asteromphalus sarcophagus* f. *obovatus*. FIGURE 27. *Asteromphalus hustedtii*. FIGURE 28. *Liriogramma petterssonii*. FIGURE 29. *Asteromphalus petterssonii*. FIGURE 30. *Asteromphalus sarcophagus* f. *pandorae*.

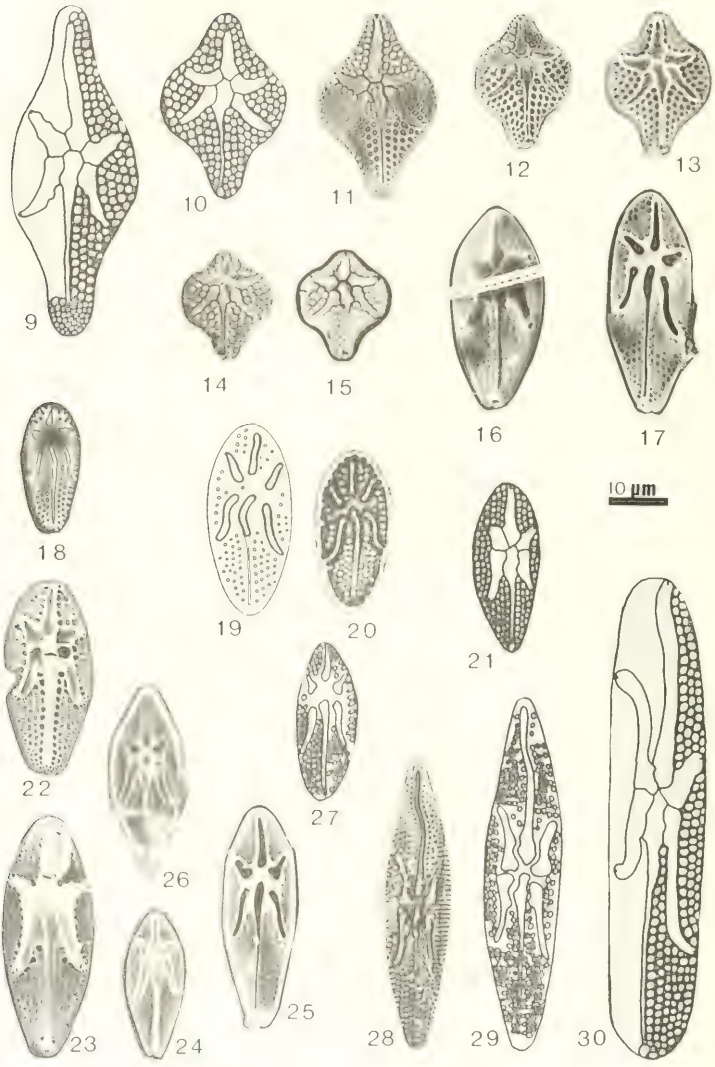
Plate 3, Figures 31–36

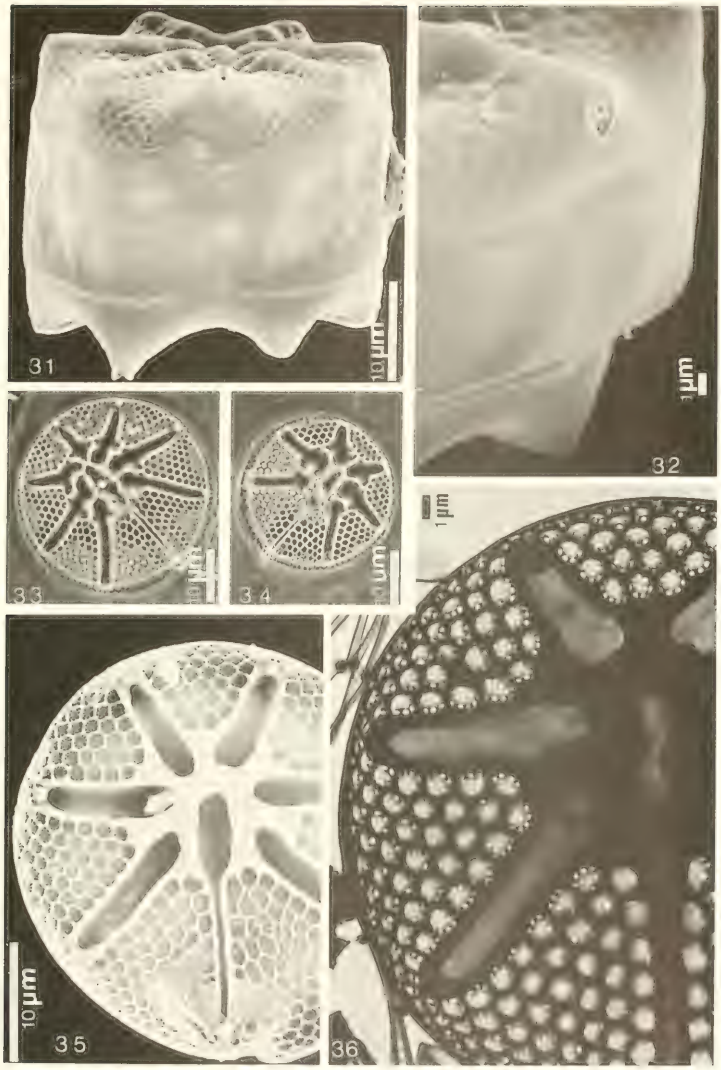
FIGURES 31–36. *Asteromphalus heptactis*. FIGURES 31–32. SEM. Each cingulum is composed of a broad and homogeneously silicified band. FIGURES 33–34. LM. Valve shape varies from subcircular to oval; the central hyaline area is always eccentric and the number of hyaline rays is variable. FIGURE 35. SEM. Internal valve view. Labiate process is located at marginal end of each ray. FIGURE 36. TEM. Internal view of a valve showing ray slit of hyaline rays and the external cribrum of areolae.

Plate 4, Figures 37–42

FIGURES 37–42. SEM *Asteromphalus heptactis*. FIGURES 37–39. Broad hyaline rays have an external marginal end section circular in shape, with its basal portion formed by two linear segments arranged at approximately 90 degrees. Central perforation of the occluding layer is bordered by one or two rings of silica, which usually appear eroded. External opening of the labiate process is evident in the basal part. FIGURES 40–41. An occluding marginal layer with central and basal perforations is also present in the narrow hyaline ray; the internal basal and lateral sides have areolae-like perforations. FIGURE 42. Marginal end section of the narrow hyaline ray is normally elongated, sometimes horseshoe-shaped.

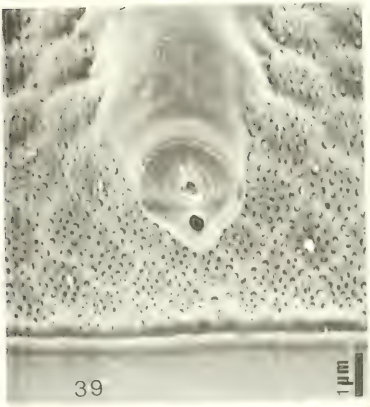

1
10 µm
2
10 µm
3
10 µm
4
10 µm
5
6
1µm
7
1µm
8
1µm

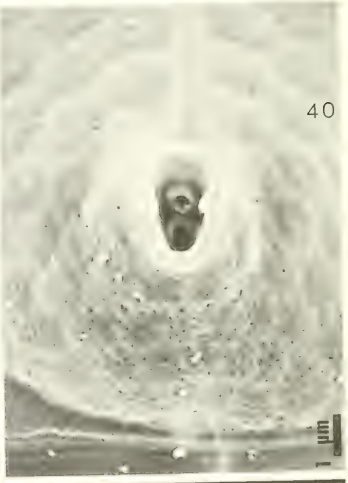

9
10
11
12
13
14
15
16
17
18
19
20
21
10 µm
22
26
27
23
24
25
28
29
30


31
10µm
32
1µm
33
10µm
34
10µm
35
10µm
36
1µm

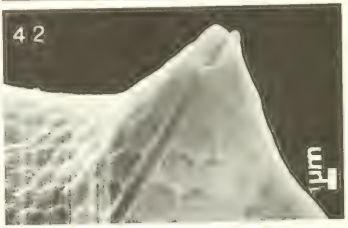
37
1µm

38
1µm


39
1µm


40
1µm

41
1µm


42
1µm

Are Both *Rhizosolenia curvirostris* Jousé and *R. barboi* Brun Found in Pleistocene Sediments of Northeastern Europe?

by

Emma Loseva

Komi Scientific Center, Ural Department,
Academy of Sciences of Russia, Syktyvkar, 167610, Russia

with 3 plates

Abstract: Marine diatom assemblages from bore-hole 1-Ja, located north of the Pechora River lowland, were examined. *Rhizosolenia* valves, formerly determined as *R. curvirostris* and *R. barboi*, were observed with light and scanning electron microscopy, and it was determined that only *R. curvirostris* was present in the assemblages. *Rhizosolenia curvirostris* is the index species for the middle Pleistocene in the Pacific. In northeastern Europe, *R. curvirostris* is characteristic of lower and middle Pleistocene sediments. This species became extinct in the region about 130 Kyr.

Introduction

Rhizosolenia curvirostris Jousé and *R. barboi* Brun are known to be index species for the Pleistocene and Pliocene, respectively, in the North Pacific. Jousé (1968) described *R. curvirostris* from sediments of the Sea of Okhotsk and the North Pacific. She restricted its upper age limit to the middle Pleistocene and emphasized that this species was absent in modern plankton and surface sediments of the Pacific.

The valve of *R. curvirostris* resembles a hollow, cylindrical, more or less curved tube with a short and wide triangular spine on the curved portion of the valve. Jousé (1971) later described *R. curvirostris* var. *inermis*, a taxon that differed from the nominate variety by its lack of a spine on the curved part of the valve. Since this variety has an age range of late Pliocene–early Pleistocene, Jousé considered it the ancestor of *R. curvirostris* var. *curvirostris*.

Later studies have shown that *R. curvirostris* var. *inermis* is a synonym of *R. barboi* Brun (Atlas of Microorganisms 1977). Akiba and Yanagisawa (1986) determined that the only difference between *R. curvirostris* and *R. barboi* is presence of a spine on the curved portion of the valve in the former species and its absence in the latter species. Jousé (1961) previously distinguished cold-water and warm-water diatom assemblages in core section 3361 in the North Pacific, over six horizons from middle Pleistocene to Holocene. Cold-water assemblages mainly contained arctoboreal and northern boreal species, while warm-water assemblages contained southern boreal species. *Rhizosolenia curvirostris* was

characteristic of all cold horizons from the middle (horizons VI and IV) to upper (horizon II) Pleistocene.

According to the stratigraphic scheme of the North Pacific, the duration of the Quaternary is 1.8 m.y. Within this interval three diatom zones are distinguished (Donahue 1970, Koizumi et al. 1980) upwards: *Actinocyclus oculatus*, *Rhizosolenia curvirostris* and *Denticula seminae*. *Rhizosolenia curvirostris* is the index species for middle Pleistocene of the North Pacific (Jousé 1969, Schrader 1973, Koizumi 1977) and northern Chukotka (Polijakova 1986), but the *R. curvirostris* zone extends up to the late Pleistocene in the North Pacific. This corresponds to the Brunhes magnetic epoch and is equal to the duration of the whole Pleistocene by the USSR schemes. The duration of the Quaternary is 0.8 m.y., and the durations of its subdivisions are—Holocene: 0–10 Kyr; late Pleistocene: 10–110 Kyr; middle Pleistocene: 110–380 Kyr; and early Pleistocene: 380–800 Kyr (Krasnor and Zarrina 1987).

Stepanova (in Slobodin and Stepanova 1986) first found both *R. curvirostris* and *R. barboi* in upper Cenozoic sediments from the northern part of the Taimir peninsula and distinguished the *R. barboi* zone in middle Pliocene in East Siberia. Later Dzinoridze registered both *R. curvirostris* and *R. barboi* in two sections in the northern part of the Pechora River lowland. She identified *R. barboi* by the absence of the spine on the valve curve and the straighter valve outlines than in *R. curvirostris*. In this way these two species were used for correlation between Pechorian and Siberian sections (Slobodin et al. 1986), resulting in the age of sediments of northeastern Europe to be considered more ancient than late Pliocene–early Pleistocene.

Results and Discussion

I had the opportunity to investigate five samples from bore-hole 1-Ja, north of Pechora River, which were provided through the courtesy of V. Zarchidze. Both light and scanning electron microscope observations were made. Observations revealed that valves are often split longitudinally, so that only one of the halves has the triangular (sometimes two-apex) spine while the other half lacks a spine (Figs. 1–12b). Therefore, halves without the spine can resemble *R. barboi* but originate from *R. curvirostris* frustules. Moreover, the degree of curvature is of no significance. This fact was not mentioned previously, although Jousé (1968) demonstrated *R. curvirostris* valves without the spine. Thus, positive identification of both species is possible only when one can see the whole valve. In my opinion, *R. curvirostris* was present only in the diatom assemblages in the samples from bore-hole 1-Ja. Hence, there is no reason to consider the sediment age to be more ancient. In the last few years single *R. curvirostris* valves or their fragments were registered in some marine early and middle Pleistocene diatom assemblages in northeastern Europe (Loseva, 1992). The upper age limit of this species together with *Thalassiosira nidulus* (Temp. and Brun) Jousé in this region is the shklovskoje interglacial of middle Pleistocene. Both of these species had become locally extinct before the moskovskoje glaciation, about 130 Kyr, while in the North Pacific their upper age limit is 276 Kyr (Sancetta and Silvestri 1984).

Thus, *R. curvirostris* is found in early and middle Pleistocene marine diatom assemblages of northeastern Europe, and its presence cannot be used to consider the age of sediments more ancient.

Literature Cited

AKIBA, F. AND V. YANAGISAWA. 1986. Taxonomy, morphology and phylogeny of the Neogene diatom zonal marker species in the middle-to-high latitudes of the North Pacific. Init. Repts. Deep Sea Drilling Project, 87:483–553.

ATLAS OF MICROORGANISMS IN BOTTOM SEDIMENTS OF THE OCEANS. 1977. "Nauka." Moscow. 32 pp.

DONAHUE, J. G. 1970. Pleistocene diatoms as climatic indicators in North Pacific sediments. Mem. Geol. Soc. Amer. 126:121–138.

JOUSÉ, A. P. 1961. Diatoms and their role in explaining ocean history. USSR Academy of Sciences, Geography Ser. 2:13–20

———. 1968. New diatom species in bottom sediments of the Pacific and the Sea of Okhotsk. News Syst. Plant. Non Vasc. 5:12–21.

———. 1969. Diatoms in Pleistocene and Late Pliocene sediments in the Boreal Pacific. Pp. 5–27 *in* Micropaleontology and organogenous sedimentation in the oceans. VIII Congres INQUA. "Nauka," Moscow. 288 pp.

———. 1971. New and interesting species of diatoms from bottom sediments of the Pacific. News Syst. Plant. Non Vasc. 8:12–18.

KOIZUMI, I. 1977. Diatom biostratigraphy in the North Pacific region. Proc. lst Congress. Pacific Neogene Stratigr. Tokyo, 235– 253.

KOIZUMI, I., J. BARRON, AND H. HARPER. 1980. Diatom correlation of Legs 56 and 57 with onshore sequences in Japan. Init. Reports. Deep Sea Drilling Project, 56–57: 687–693.

KRASNOV, I. I. AND E. P. ZARRINA. 1987. The interregional stratigraphic scheme of Quaternary sediments of east-European platform and its comparison with other geochronological scales. Pp. 19–23 *in* Cenozoic sediments origin and structural geomorphology of the USSR. XII Congress INQUA. Leningrad.

LOSEVA, E. I. 1992. Atlas of marine Pleistocene diatoms of northeastern European part of the USSR. "Nauka." Leningrad.

POLIJAKOVA, E. I. 1986. Ecological and systematical characteristic of upper Cenozoic diatom flora of northern Chukotka. Pp. 79–83 *in* Urgent questions of modern palaeoalgogy. Kiev.

SANCETTA, C. AND S. SILVESTRI. 1984. Diatom stratigraphy of the Late Pleistocene (Brunhes) Subarctic Pacific. Mar. Micropaleontolgy 9:263–274.

SCHRADER, H-J. 1973 Cenozoic diatoms from the northeastern Pacific. Init. Reports. Deep Sea Drilling Project 18:673–797.

SLOBODIN, V. Ya., N. I. DRUZHININA, AND G. V. STEPANOVA. 1986. Correlation of the Neogene marine sediments in the Arctic from biostratigraphical data. Pp. 196–198 *in* Reports of the 10th micropaleontological conference of the USSR. Zonal Stratigraphy based on Microorganisms and Methods of its Development. Leningrad.

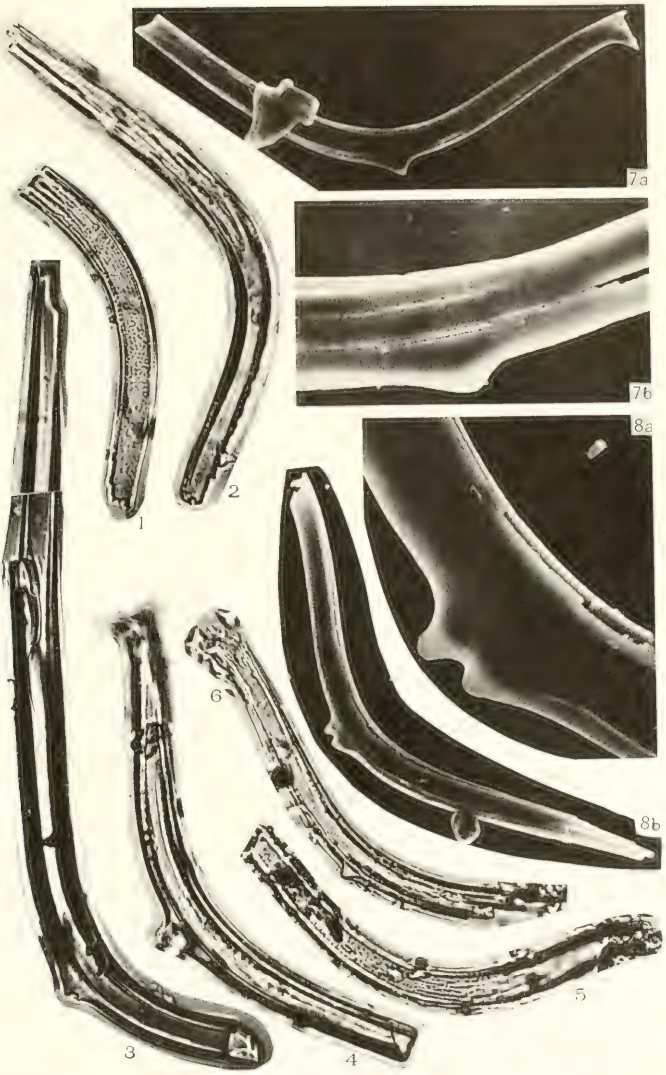
SLOBODIN, V. Ya. AND G. V. STEPANOVA. 1986. Stratigraphy and paleogeography of the Cenozoic of Northern Taimir. Pp. 110–113 *in* Cenozoic of the shelf and islands of the Soviet arctic. Leningrad.

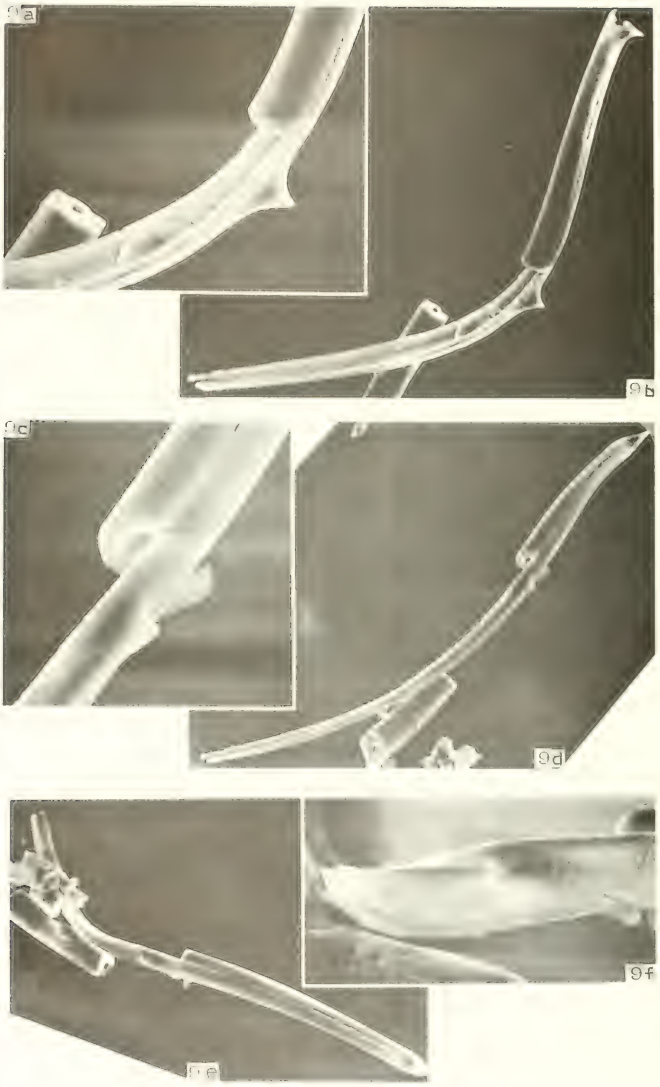
Explanation of Plates

Plate 1, Figures 1–8
FIGURES 1–8. *Rhizosolenia curvirostris*. FIGURES 1–6. LM × 1000. FIGURES 7, 8. SEM. External view. FIGURES 7a, 8b. × 1000. FIGURES 7b, 8a. × 3300

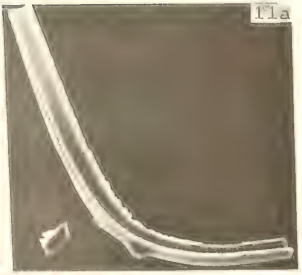
Plate 2, Figures 9a–f
FIGURES 9a–f. *Rhizosolenia curvirostris*. SEM. Broken frustule. FIGURES 9b, d, e. × 1000. FIGURE 9a. × 2000. FIGURES 9c, f. × 3300.

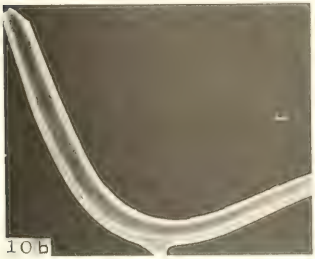
Plate 3, Figures 10–12
FIGURES 10a–12b. *Rhizosolenia curvirostris*. SEM. Internal view. FIGURES 10a, b, 11a, 12a. × 1000. FIGURES 11b, c. × 3300. FIGURE. 12b. × 4700.

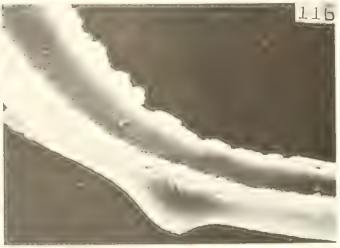

7a
7b
8a
8b
1
2
3
4
5
6


♀a
♀b
♀c
♂d
♂e
♂f

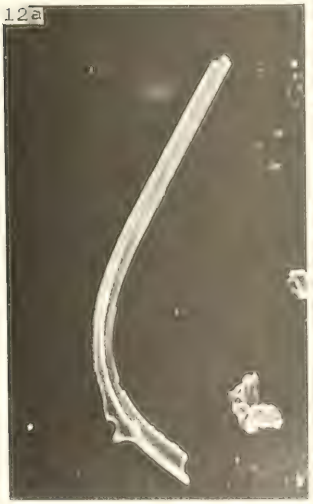
10a


11a


10b


11b

11c


12a

12b

Valve Morphology of *Coscinodiscus janischii* Schmidt (Bacillariophyceae)

by

Martha E. Ferrario and Eugenia A. Sar

Division Ficologia, Facultad de Ciencias Naturales y Museo,
Universidad Nacional de La Plata, Paseo del Bosque s/n 1900, La Plata, Argentina

with 1 plate

Abstract: *Coscinodiscus janischii* Schmidt from Puerto Madryn (Chubut) and Puerto Brown (Tierra del Fuego), Argentina, was studied with light and scanning electron microscopy. Clear differences between *C. janischii* and similar species *C. gigas* Ehrenberg and *C. wailesii* Gran and Angst were observed. Our results show that *C. janischii* fits the description of *Coscinodiscus sensu stricto*, although some of the areolae have distinctive characteristics not previously observed in the genus.

Introduction

The genus *Coscinodiscus* Ehrenberg, with about 400 validly described taxa (Van Landingham 1968), has been revised extensively in the last two decades, based upon observations made with the scanning electron microscope. The result of these revisions has been that many *Coscinodiscus* species have been placed in other genera. In particular, *Thalassiosira* has been expanded through many published studies, including the early works by Hasle (1968) and Fryxell and Hasle (1974).

Simonsen (1975, 1979) established three morphologic groups within the genus *Coscinodiscus*, based on the pattern of labiate processes. Rapid progress in developing a concept of the genus took place following publication of Simonsen's hypotheses. In accordance with Ross and Sims (1973), Fryxell (1978) proposed *Coscinodiscus argus* Ehrenberg as the generictype. Further studies resulted in the splitting of some species of this genus into several others, including: *Psammodiscus* Round and Mann (Round and Mann 1980), *Thalassiosiropsis* Hasle (Hasle and Syvertsen 1985), *Stellarima* Hasle and Sims (Hasle and Sims 1986a), and *Azpeitia* M. Peragallo (Fryxell et al. 1986). Subsequent to the above studies, Hasle and Sims (1986b) emended the diagnosis of the genus *Coscinodiscus*. Finally, and with the purpose of introducing more precise limits among the species, Fryxell and Ashworth (1988) included additional ultrastructural diagnostic characters to the ones classically employed.

In this paper we study the valvar morphology of *Coscinodiscus janischii* Schmidt in order to analyze the position of this species in the genus *C. sensu stricto*. Comparisons are made with the nearest species, *C. gigas* Ehrenberg and *C. wailesii* Gran and Angst.

Materials and Methods

Marine neritic phytoplankton was collected in 50 µm mesh plankton nets from two sites in neritic Argentinian waters: Puerto Madryn, Chubut, 29 Sept. 1981 (sample no. 3621), and Puerto Brown, Tierra del Fuego, 24 Feb. 1963 (sample no. 2396). The samples were preserved in buffered formalin. They were subsequently cleaned of organic matter (Hasle and Syvertsen 1980), and subsamples were mounted in Hyrax for study in a Wild M20 phase contrast light microscope. Other subsamples were mounted on glass coverslips attached to aluminum stubs, sputter coated with gold, and examined under a JEOL JSM T100 scanning electron microscope. The material was added to the collection of the Division Ficologia, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata as "Diatoms from Chubut" and "Diatoms from Tierra del Fuego."

The above material was compared with slides 91, 148, 182, 551, and 848 from the Tempère and Peragallo Collection, 2nd Edition (Tempère and Peragallo 1915) and with slide series 167 from the Frenguelli Collection.

Results

Coscinodiscus janischii Schmidt, 1878
(Pl. 64, Figs. 3, 4)

Cells solitary, coin shaped, 160–240 µm in diameter, 35–40 µm deep about the pervalvar axis. Valves flat, sharply elevated in the marginal area. Areolae pattern radial with spiralling secondary rows more or less evident (Fig. 1). Central area small, hyaline, without any aperture, sharply delimited in the interior part with randomly distributed siliceous granules and bundles of linear markings radiating from its margin (Figs. 3, 6).

Areolae ordered in complete and incomplete rows, the latter originating towards the midradius. Central areolae elongated in radial direction (Figs. 2, 3), 2.5–3.5 in 10 µm. Areolae diminishing in size towards the margin, 4–4.5 in 10 µm, becoming loculated and hexagonal only near the periphery (Figs. 4, 9). External cribra delimited by a solid siliceous covering except in the mantle where they are continuous (Figs. 7, 10). Pores of the cribra closed by very delicate sieves, the cribrella (Figs. 3, 8), which are often destroyed during cleaning.

Valve mantle vertical, possessing two rings of areolae with continuous cribra cover and siliceous ridge-like irregularities around their margins (Fig. 10). Microrimoportulae placed in one ring on the mantle, 2–4 areolae distant, 2 in 10 µm (Fig. 12). Two macrorimoportulae, 120–135 ° apart, located in or close to the ring of microrimoportulae (Fig. 11).

Data about the distribution of this species along the coast of Argentina are reported elsewhere (Ferrario 1981).

Comparisons With Other Material

Coscinodiscus janischii from the Tempère and Peragallo Collection was scarce and generally broken. Specimens were markedly similar to the cells observed along the Argentine coasts, particularly with respect to the following: diameter, general view of the valve with a narrow outstanding marginal area with hexagonal areolae, areolae pattern, density and shape, and type of central area.

Comparison with the Frenguelli material (Frenguelli 1928) allowed us to establish clear differences with respect to general view of the valve, type of central area, and size and shape of the areolae in different parts of the valve.

Discussion and Conclusions

The analysis of some classical works, such as Schmidt (1878, pl. 64, Figs. 3, 4), Rattray (1890:543), Peragallo and Peragallo (1897–1908:432, pl. 118, Fig. 4), and Hustedt (1928:459, Fig. 257) allowed us to establish similarities between the observations on our material and the descriptions and illustrations of these authors. The comparison was made following the classic criteria that emphasized areolae size and array, presence or absence of a particular structure in the central area, and diameter and general aspect of the valves.

As can be seen from our results, we assume the material from Puerto Madryn and Puerto Brown to be conspecific with the material in the Tempère and Peragallo Collection. Based on this conclusion we consider the differences with Hustedt's illustrations to be a difference in drawing, since this author takes into account the material from the Tempère and Peragallo Collection.

In accordance with the criteria of Rattray (1890) and Takano (1976) among other authors discussed, we have noticed that *Coscinodiscus janischii* easily can be confused in the light microscope with other large species, such as *C. gigas* and *C. wailesii*. Because of the similarities we think it useful to establish the most outstanding differences between these taxa.

Coscinodiscus gigas does not have the narrow and clear marginal area observable in the light microscope. Areolae are smaller in the center and increase in size towards the periphery. Microrimoportulae are closer to one another and located in the transition between the mantle and valve surface (Takano 1976:134, Figs. 5, 6). Macrorimoportulae are relatively smaller and less coiled (Takano 1976, Figs. 14–16); Fryxell and Ashworth 1988, Fig. 28), and the mantle is deeper with a lattice pattern of hexagonal areolae (Takano 1976, Figs. 5, 6; Fryxell and Ashworth 1988, Fig. 24).

Coscinodiscus wailesii was recently examined by Schmid and Volcani (1983). According to their paper *C. wailesii* does not have a narrow marginal area (LM). Areolae are smaller, almost regular in size throughout the valve, and always hexagonal (Schmid and Volcani 1983:388, Figs. 2, 3). There are no solid siliceous coverings enclosing the external cribra of the areolae (Schmid and Volcani 1983, Fig. 30). The central area is larger with bundles of siliceous thickenings reaching the margin (Schmid and Volcani 1983, Fig. 2). Microrimoportulae have a very different distribution pattern, being scattered on the valvar surface as well as being present in a ring at the juncture of the mantle and valve and in an additional ring in the free border of the mantle (Schmid and Volcani 1983, Fig. 10).

The results obtained on the valvar morphology of *C. janischii* allow us to include this species in the genus *Coscinodiscus sensu stricto*, taking into account the limits established by Hasle and Sims (1986b) for the emended genus. However, the presence of poroid-like areolae (Fig. 5) on the surface of the material studied suggests the need to widen the limits of variability of areolar structure in the genus.

Acknowledgements

We are grateful to Dr. A. M. Schmid for her active and generous participation in the comparison between our material and *C. wailesii*.

Literature Cited

FERRARIO, M. E. 1981. Diatomeas Centrales de la Ria de Puerto Deseado, Santa Cruz, Argentina. V. Fam. Coscinodiscaceae y Biddulphiaceae. Lilloa 35:115–123.

FRENGUELLI, J. 1928. Diatomeas del Oceano Atlantico frente a Mar del Plata (Republica Argentina). An. Mus. Nac. Hist. Bernardino Rivadavia 34:497–572.

FRYXELL, G. A. 1978. Proposal for the conservation of the diatom *Coscinodiscus argus* Ehrenberg as the type of the genus. Taxon 27:122–125.

FRYXELL, G. A. AND T. K. ASHWORTH. 1988. The diatom genus *Coscinodiscus* Ehrenberg: characters having taxonomic value. Bot. Mar. 31:359–374.

FRYXELL, G. A. AND G. R. HASLE. 1974. Coscinodiscineae: some consistent patterns in diatom morphology. Nova Hedwigia Beih. 45:69–96.

FRYXELL, G. A., P. A. SIMS, AND T. P. WATKINS. 1986. Azpeitia (Bacillariophyceae): related genera and promorphology. Syst. Bot. Monogr. 13:1–74.

HASLE, G. R. 1968. The valve processes of the centric diatom genus *Thalassiosira*. Nytt. Mag. Bot. 15:193–201.

HASLE, G. R. AND P. A. SIMS. 1986a. The diatom genera *Stellarima* and *Symbolophora* with comments on the genus *Actinoptychus*. Br. Phycol. J. 21:97–114.

———. 1986b. The diatom genus *Coscinodiscus* Ehrenberg Bot. Mar. 29:305–318.

HASLE, G. R. AND E. E. SYVERTSEN 1980. The diatom genus *Cerataulina*: morphology and taxonomy. Bacillaria 3:79–113.

———. 1985. *Thalassiosiropsis*, a new diatom genus from the fossil records. Micropaleontology 31:82–91.

HUSTEDT, F. 1928. Die Kieselalgen Deutschlands, Österreichs und der Schweiz mit Berücksichtigung der ubrigen Länder Europas sowie der angrenzenden Meeresgebeite. Pp. 273–478 *in* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, L. Rabenhorst, ed. Akad. Verlags., Leipzig.

PERAGALLO, H. AND M. PERAGALLO. 1897–1908. Diatomées Marines de France et des Districts Maritimes Voisins. Micrographe Editeurs, a Grenz-sur-Loing. 491 pp.

RATTRAY, J. 1890. A revision of the genus *Coscinodiscus* Ehrb., and of some allied genera. Proc. R. Soc. Edinburgh 6:449–692.

ROSS, R. AND P. A. SIMS. 1973. Observations on family and generic limits in the Centrales. Nova Hedwigia Beih. 45:97–121.

ROUND, F. E. AND D. G. MANN. 1980. *Psammodiscus* nov. gen. based on *Coscinodiscus nitidus*. Ann. Bot. 46:367–373.

SCHMID, A. M. AND B. E. VOLCANI. 1983. Wall morphogenesis in *Coscinodiscus wailesii* Gran and Angst. I. Valve morphology and development of its architecture. J. Phycol. 19:387–402.

SCHMIDT, A. 1874–1944. Atlas der Diatomaceen-Kunde. R. Reisland, Leipzig.

SIMONSEN, R. 1975. On the pseudonodulus of the centric diatom, or Hemidiscaceae reconsidered. Nova Hedwigia Beih. 53:83–94.

———. 1979. The diatom system, ideas on phylogeny. Bacillaria 2: 9–71.

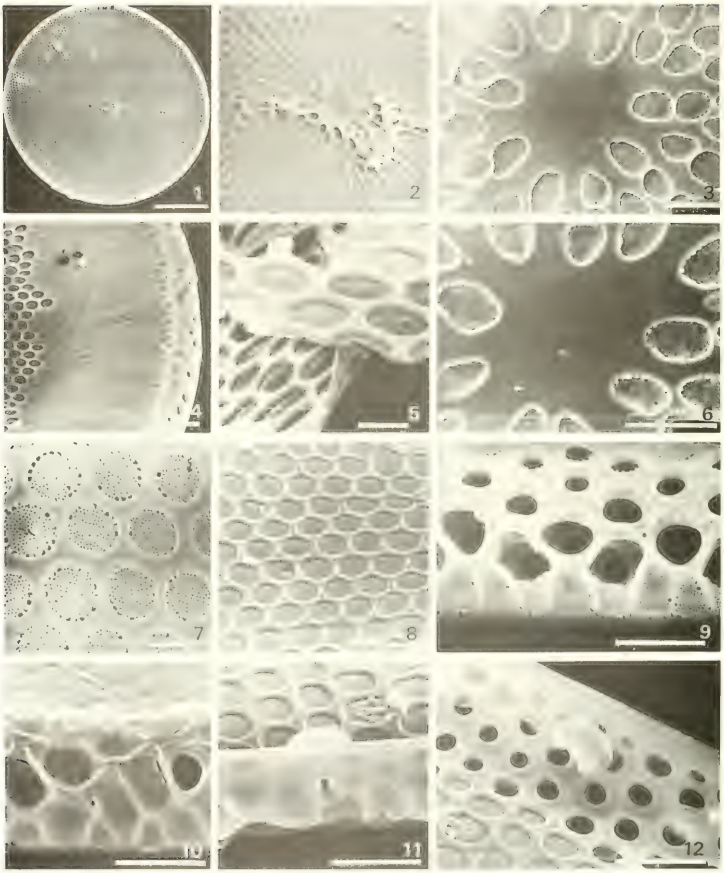
TAKANO, H. 1976. Scanning electron microscopy of diatoms. III. *Coscinodiscus gigas* Ehrenberg. Bull. Tokai Reg. Fish. Res. Lab. 88:133–141.

VAN LANDINGHAM, S. L. 1968. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Part II. *Bacteriastrum* through *Coscinodiscus*. J. Cramer, Vaduz. 494–1086 pp.

Explanation of Plate

Plate 1, Figs. 1–12

FIGURES 1–12. *Coscinodiscus janischii*. FIGURE 1. Valvar surface showing elevated marginal area and radial areolae pattern with spiralling secondary rows (internal view). Scale bar = 50 μm. FIGURE 2. Central area showing randomly distributed siliceous granules and bundles of linear markings radiating from its margin (internal view). Scale bar = 10 μm. FIGURE 3. Areolae around central area elongated in radial direction, showing polygonal cribral pores closed by cribrella (internal view). Scale bar = 5 μm. FIGURE 4. Marginal area with areolae becoming hexagonal only near the periphery. Scale bar = 10 μm. FIGURE 5. Broken valve showing structure of areolae. Scale bar = 2 μm. FIGURE 6. Central area (external view). Scale bar = 5 μm. FIGURE 7. Cribra of circular areolae delimited by solid siliceous covering (mid-radius, external view). Scale bar = 2 μm. Figures 8–12: Scale bar = 5 μm. FIGURE 8. Circular areolae (mid-radius, internal view). FIGURE 9. Detail of the loculate areolae in marginal region. FIGURE 10. Mantle showing a microrimoportula opening surrounded by continuous cribral coverage. FIGURE 11. External opening of a macrorimoportula surrounded by continuous cribral coverage. FIGURE 12. Interior of mantle showing a macrorimoportula and the neighboring microrimoportulae.


1
2
3
4
5
6
7
8
9
10
11
12

Genetic Structure of Microalgal Populations. I. Problems Associated With the Use of Strains as Terminal Taxa

by

Jane C. Gallagher

Department of Biology, City College of C.U.N.Y.
Convent Ave. at 138th St., New York, New York 10031

with 8 figures and 3 tables

Abstract: Two approaches to sampling have been developed for the examination of the distribution of characters for phylogeny reconstruction and the classification of diatoms and other microalgae. The first is the traditional microbiological method where a small number of strains isolated from widely spaced environments are compared. This approach is used mostly for physiological and molecular characters. The levels of divergence among individual strains are then interpreted in relation to differences in similar parameters obtained from terrestrial organisms. The alternative approach is the population method where large numbers of strains are examined from both contiguous and widely spaced environments. This approach is commonly used for studies of morphology, but rarely for molecular data. Thus, the difference between morphological and molecular studies of phylogeny is not simply due to different types of characters, but is also due to different sampling strategies. The effect of these two sampling strategies on interpretations of evolutionary relationships was explored by analysis of a data set available for the temporal and spatial genetic structure of the Narragansett Bay populations of *Skeletonema costatum* (Grev.) Cleve. Cladistic and distance measures were compared. The results demonstrate that if all 457 strains are compared in an analysis using the strains as terminal taxa, then it is not possible to recover the patterns of seasonal genetic variation. It is only when groups of strains are compared that patterns can be discerned. Recommendations are made for sampling strategies for molecular evolutionary studies of diatoms.

Introduction

The genetic structure of microalgal populations and species is the result of the combined effects of selection, drift, migration, and mutation, which are mediated by the historical and biological factors particular to each taxon. The pattern of genetic structure determines, in part, the taxon's responses to changes in its environment (Loveless and Hamrick 1984).

Over the last 30 years intraspecific variation has been documented for almost all parameters hypothesized to govern the ecological success of organisms (see Gallagher 1986; Wood 1987; Brand 1990, for reviews). The results of virtually all of these investigations support the hypothesis that the genetic diversity within and among species of microalgae is greater than that found within and among species of higher organisms (Olsen 1990). For example, 30–60% of enzyme loci tested by gel electrophoresis are monomorphic (invariant) among

species within genera of higher organisms (Avise 1975; Ferguson 1988). However, no monomorphic enzyme loci have ever been detected among strains within species of microalgae.

Although the existence of intraspecific variation is well-documented for every type of microalga, the spatial and temporal scales of differentiation have rarely been quantified (see Gallagher 1986; Brand 1990, for reviews). This lack of information is largely the result of sampling methods developed for microorganisms. Traditional microbiological sampling methods examine one or two strains isolated from several distantly spaced environments. These strains are tested for one or more parameters, and the results are usually extrapolated to the entire population present in the ecosystem from which the strain was obtained. This approach treats strains as terminal taxa that are assumed to be representative of the population from which they were isolated or of a phylogenetic group. Natural selection is usually invoked to account for differences among the putative groups that the strains are supposed to represent. In some cases the pattern of differences among strains is interpreted to indicate species level differences and new taxa are described. In other cases, the differentiation among strains shows no discernable pattern, and these data are used to cast doubt on morphological classifications (e.g., Hayhome et al. 1989). The presence of intragroup diversity confounds such conclusions. For example, consider the case in which a single, genetically diverse population extends over a wide area. The presence of genetic differences between two strains isolated from different locations might lead to the conclusion that there are two distinct populations. In this case, the discontinuity among small numbers of strains obtained using a microbiological sampling strategy can force interpretations of ecological or evolutionary discontinuities where none exist.

A sampling strategy based on the use of single strains as terminal taxa is fundamentally different from the population methods used for morphological analyses. The use of single strains as terminals is propelled by the current interest in the use of molecular methods in systematics and population biology because many of these methods are too expensive and time-consuming to apply to large samples. Thus, the difference between morphological and molecular studies is not simply one of comparing different types of characters, but is also one of comparing different types of sampling strategies. This difference can create serious problems in the interpretation of data. The goal of this paper is to illustrate some of these problems and to suggest some solutions.

The effects of large versus small sample sizes and the use of populations versus strains as terminal taxa can be illustrated by an reexamination of the data set available for allozyme diversity in the Narragansett Bay populations of *Skeletonema costatum* (Grev.) Cleve. The banding patterns of 457 strains of this species were examined, and it was demonstrated that the frequency of different types of strains varied with season (Gallagher 1979; 1980). The extreme genetic differentiation between the summer and winter forms is mediated by the existence of genetic and physiologically intermediate populations that are most abundant in the interbloom period (Gallagher 1982). A recent reexamination of some unpublished data also demonstrates that space is also important in determining population structure and that these two variables are not independent (Gallagher, in prep.). These studies used populations as the terminal taxa and the patterns of differentiation among them are shown in Figure 1 for a cladistic analysis of the data set. The effect of using single strains as terminal taxa can be determined by resampling the individual ermine if some or all of the patterns shown in Figure 1 can be recovered.

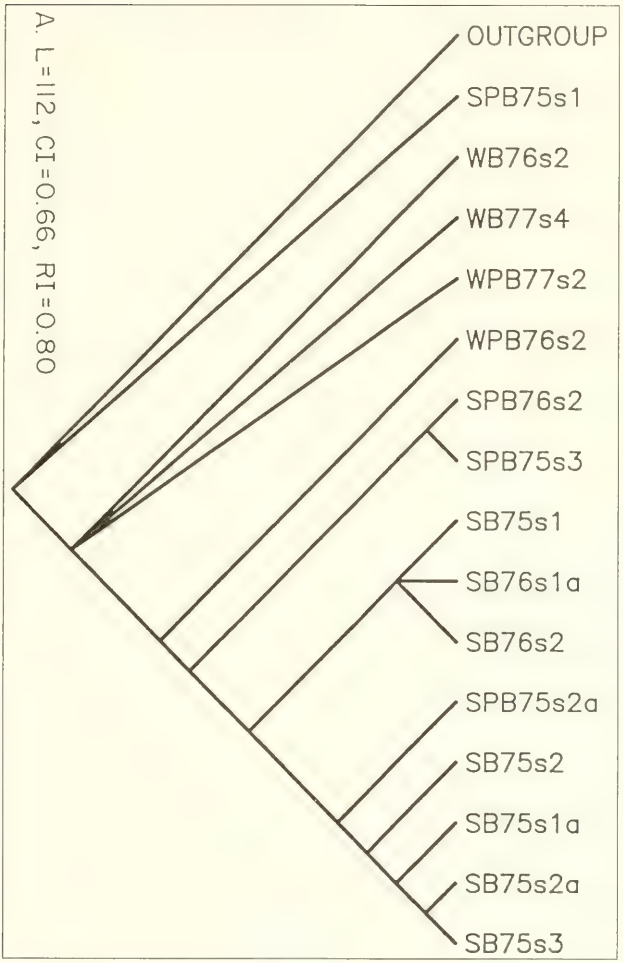


FIGURE 1. Cladistic analysis of populations of *Skeletonema costatum* in Narragansett Bay, R. I., using the independent allele model and presence/absence coding of different alleles in a sample. Sample coding: SPB = summer prebloom samples; WPB = winter prebloom samples; SB = summer bloom samples; WB = winter bloom samples; 75 = 1975; 76 = 1976; 77 = 1977; s1, s1a, s2, s2a, s3 = stations 1 through 3 from north to south within the bay. For example, SPB75s1 is the summer prebloom sample for 1975 at station 1. Strict consensus tree of 10 equally parsimonious trees obtained with successive weighting.

Materials and Methods

The details of sampling the strains and electrophoresis are described in detail in Gallagher (1980, and in prep). Briefly, individual strains were isolated by micropipet from unenriched natural seawater samples and were each placed in separate test tubes of f/2 medium (Guillard and Ryther 1962). The sampling strategy was to obtain sample sizes of approximately 50 strains from a mid-bay station two weeks prior to and during the winter and summer blooms of *S. costatum* for two consecutive years starting in the summer of 1975. During the summers of 1975 and 1976, additional samples were taken in the bay at different locations to ascertain the effect of spatial differentiation on population structure. Great care was taken to treat all isolates in an identical manner and for most samples the survival of isolates was very high. This high survival rate validated the extrapolation of frequencies of different types of strains in the samples to the natural populations from which they were isolated.

Strains were categorized according to their allozyme banding patterns at five enzyme loci: phosphoglucose isomerase (PGI), malate dehydrogenase (MDH), glutamate dehydrogenase (GDH), and two loci of superoxide dismutase (TO1 and TO2). Strains were grown for electrophoresis under identical conditions regardless of the initial conditions at the time of isolation in order to eliminate environmental effects on gene expression. In addition, a selection of genetically different strains was grown under a variety of conditions to determine if banding patterns changed with environment. Only invariate loci were used. Under these specific conditions, the differences in banding patterns among strains were assumed to reflect underlying genetic differences. Banding patterns were interpreted as alleles at each locus and were converted into genotype by assuming that *S. costatum* is diploid. A previous analysis of this data set divided the strains into broad groups and the terminology is retained here for convenience (Gallagher 1982). The WH and Whet groups have the most common alleles present in winter populations at all four seasonally variant loci. These groups are also minor components of summer populations. The SH group has the most common summer bloom alleles at all four loci that show changes in frequency with season. The "Mixed" and "Rare" groups are heterogeneous groups that have common summer alleles at some loci and winter alleles at the remainder. They are physiological and genetic intermediates between the extremes represented by the summer and winter blooms (Gallagher 1982).

For cladistic analyses, each band (allele) was coded as a separate, individually segregating character whose presence or absence was scored without assigning it to a locus. Homology among bands found in different organisms and samples was based on identical mobilities (Rf values) and reactivity using a particular staining protocol. This coding approach has been termed the Independent Allele Model (Mickevich and Johnson 1976; Mickevich and Mitter 1983; Buth 1984). Forms of this coding method have also been used in many phenetic interpretations of banding patterns in microalgae (e.g., Soudek and Robinson 1983; Hayhome and Pfiester 1983; Cembella et al. 1988; Hayhome et al. 1989). Cladograms were calculated using the Hennig86 program (Farris 1988). Trees were rooted using an all zero outgroup. This method maximizes the overall congruence of characters in the ingroup. The fit of the input data to the cladogram is measured by the consistency index (CI) which is calculated as:

$$CI_i = S_i/P_i$$

where S_i is the number of steps for character i implied from the data and P_ii is the number of steps in the tree. The overall CI for the tree is the sum of character ranges divided by

the total number of steps in the tree (Farris 1989). The retention index (RI) is a measure of the degree to which a character is synapomorphic and is calculated as:

$RI_i = (h_i - s_i)/(h_i - l_i)$

where h_i is the maximum number of steps for character i, s is the observed number of steps in the tree and l is the minimum number of steps (Farris 1989). A character that is an autapomorphy (unique to one taxon) has an RI of 0 and one that is perfectly synapomorphic and has no homoplasy has an RI of 1.0.

Cladograms were calculated using both unweighted characters and with the successive weighting protocol of Hennig86 in order to determine which technique gave greater resolution (Farris 1989). The latter technique has the advantage of providing a means of basing groups on more reliable characters without making prior decisions on weighting. Weights are calculated from the best fits, as determined by the product of the character consistency and retention indices and are then scaled to lie in the range 0–10 (Farris 1988).

Distance coefficients were calculated between pairs of strains using Jaccard's coefficient (Sneath and Sokal 1973). This is a simple matching coefficient calculated by:

$S_j = [a/(a + u)] \times 100$

where u is the number of mismatches and a is the number of matches between the banding patterns. This was converted to a distance coefficient by subtracting it from 100.

The distance matrix was used as input to a distance tree calculated by the Fitch-Margoliash method (program FITCH in the PHYLIP package) (Fitch and Margoliash 1967; Felsenstein 1985). This method constructs a tree by successive addition of each sample and then attempts to optimize the overall fit of the distances among samples in the tree to the distances in the input matrix by rearranging the branches. The fit is assessed by minimizing the sum of squares of the differences between the distances represented in the tree and the input distances. The original Fitch-Margoliash method allowed the tree to be fit with negative branch lengths; the Felsenstein implementation uses a minimum branch length of zero. The position of a midpoint root, the point midway between the two most distant taxa, (Farris 1972) was calculated for each tree.

Results

A companion paper (Gallagher, in prep.) provides the details of a comparison of methods of data analysis using groups of strains (populations) as terminal taxa and a variety of coding methods. This analysis showed that cladistic analyses using the Independent Allele Model and successive weighting was effective in analyzing the data. Fitch-Margoliash trees had the best fits for the distance analyses and were used to build trees here. Phylogenetic systematics offers a better system for the analysis of different types of data and is recommended. However, the distance analyses were included here in order to demonstrate that the problems inherent in the use of single strains as terminal taxa are common to both methods of analysis.

Several sets of analyses were run using subsamples of the Narragansett Bay data set. Seven are shown here to illustrate the general pattern of results.

Figure 2 illustrates a cladogram of the most parsimonious tree calculated using 13 randomly chosen strains from the summer prebloom sample of 1975 as input. Successive weighting improved resolution of the tree. Two major groups were identified. The larger of the

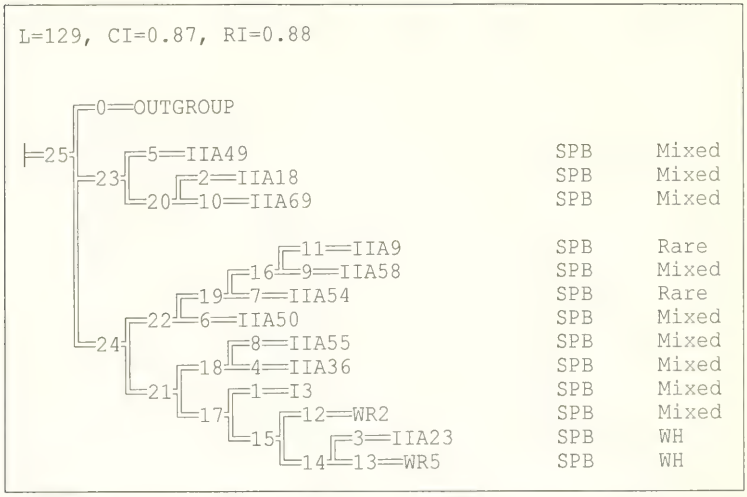


FIGURE 2. Most parsimonious tree calculated using strains from the summer prebloom of 1975 from station 2a and successive weighting. The designation beside each strain is the season of isolation (SPB) and the genetic group of each strain according to the classification of Gallagher (1982) (see text).

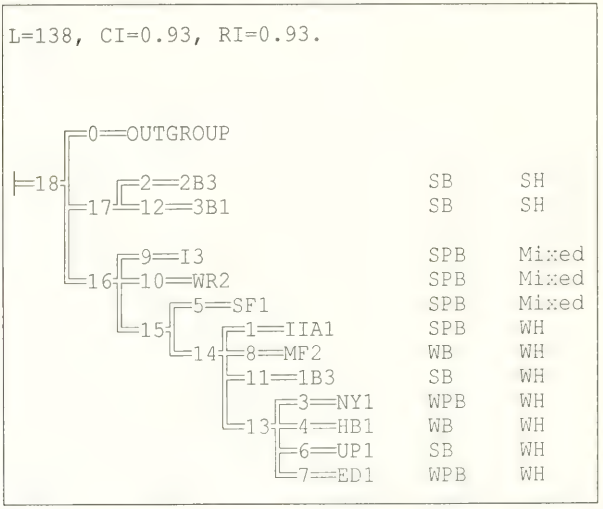


FIGURE 3. Strict consensus of two equally parsimonious trees obtained using the first stain isolated from each seasonal sample as input and successive weighting.

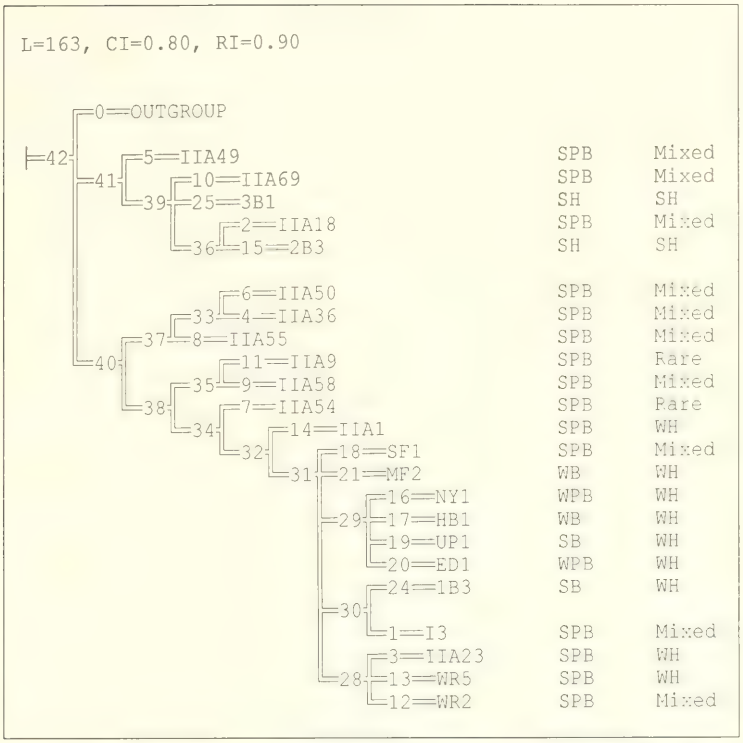


FIGURE 4. Most parsimonious tree obtained using the strains included in Figures 2 and 3 and successive weighting.

two clades subdivides at nodes 21 and 22 into two subgroups. The Mixed strains were found in all of the clades.

Figure 3 shows a cladogram of the consensus tree calculated using successive weighting and the first strain isolated from each seasonal sample as input. Two main clades emerge from the analysis. The first at node 17 is from the summer bloom and the second is comprised of mixed and WH types. The strains are clearly separated by genotype, but not by time of isolation. Strains with the most common winter genotypes are also present in summer samples, and two of them were included in this analysis by chance. Strains I3 and WR2 were included in both of the analyses depicted in Figures 2 and 3.

Figure 4 illustrates a cladogram of all of the strains used in the first two analyses. The complete data matrix for this analysis is shown in Table 1. In this cladogram, two main groups again appear. However, the topologies are not simple additions of the first two cladograms. The position of various strains changes dramatically. The nature of the changes can be illustrated by the positions of strains I3 and WR2. In Figure 3 these strains were

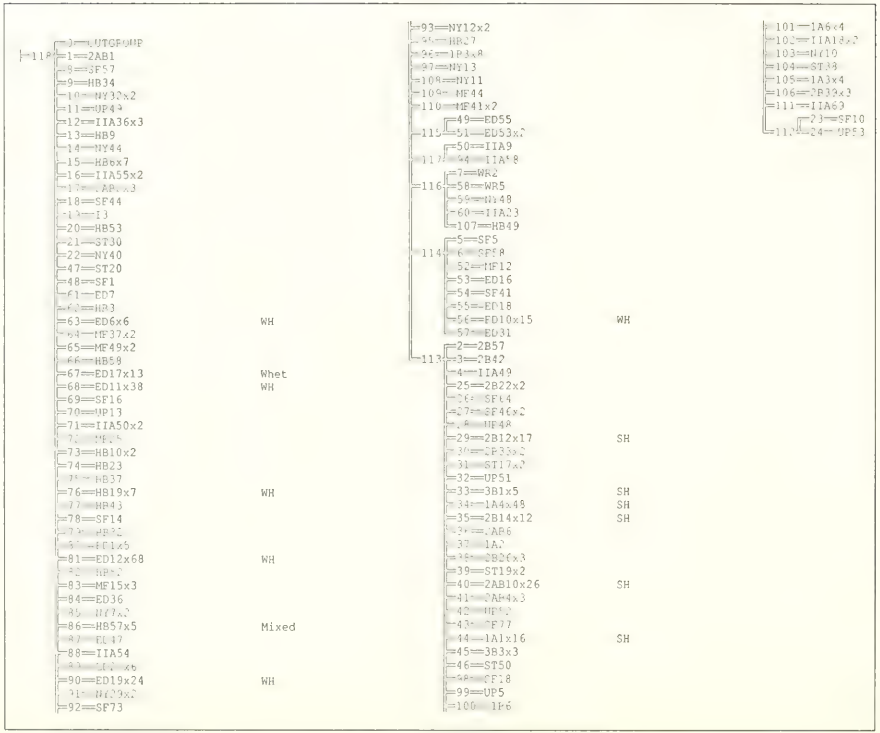


FIGURE 5. Strict consensus of 100 equally parsimonious trees obtained using successive weighting and the entire Narragansett Bay data set as input. Length = 100, CI = 0.61, RI = 0.95

TABLE 1. Data matrix for cladistic analysis of strains of *Skeletonema costatum* using the Independent Allele Model.

Strain	Allele																							
	A_1	A	B	C	J	K	L	M	N	E_1	E	F	F_1	G	H	I	T_1	T	U	V	W	X	P	Q	R
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I3	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1
IIA18	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
IIA23	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1
IIA36	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
IIA49	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
IIA50	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0
IIA54	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1
IIA55	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0
IIA58	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0
IIA69	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0
IIA9	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0
WR2	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1
WR5	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1
IIA1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
2B3	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
NY1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1
HB1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1
SF1	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1
UP1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1
ED1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1
MF2	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
1B3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
3B1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0

TABLE 2. Inferred genotypes of strains used in the distance analyses. Each letter refers to an allele at each locus.

	Locus				
Strain	PGI	MDH	GDH	TO1	TO2
IIA1	BB	KK	HH	UU	RR
2B3	AA	MM	GG	XX	PP
NY1	BB	KK	GG	UU	RR
HB1	BB	KK	GG	UU	RR
SF1	AB	KK	FF	UU	RR
UP1	BB	KK	GG	UU	RR
ED1	BB	KK	GG	UU	RQ
MF2	BB	KK	EE	UU	RR
I3	AA	KK	II	T_1U	PR
WR2	AA	KK	F_1F_1	UU	RQ
3B1	AA	MM	GG	VV	PP
1B3	BB	KK	II	UU	RR
IIA4	AA	MM	GG	WW	PP
IIA9	BB	JK	HH	XX	PP
IIA10	AA	MM	GG	WW	PP
IIA11	BB	KK	GG	UU	RR
IIA12	AA	MM	GG	WW	PP

at the base of the second clade, whereas in Figure 4 they are the unresolved sister group of the WH strains. Similar changes in branching order can be seen by the change in position of strain IIA36 and IIA50. In none of these three cladograms can patterns of change with season be clearly delineated.

Figure 5 depicts the consensus cladogram of all of the 457 strains using successive weighting. This cladogram must be regarded as an approximate result because so many equally parsimonious trees were generated that the capacity of the program was exceeded. For this analysis categories of strains with more than one representative were tallied together. For example, one strain had a banding pattern identical to that of strain NY32 and both strains are represented as NY32x2 at node 10. The total strains fell into 112 categories, 46 categories had more than one strain and 19 categories had more than five strains. The total analysis had very little resolution, and many of the groups of strains in the most common winter category appeared as unresolved sister taxa. Several strains with only a single representative grouped together. Most the the common summer bloom categories (SH) also appeared as unresolved sister taxa at node 113. Although the summer and winter categories show a weak separation, there is no clear evidence of seasonal changes in frequencies. The consistency index declined from 0.87 in Figure 2 to 0.61 in Figure 5.

Figures 6–8 show distance trees calculated for successively increasing numbers of strains. The genotypes of the strains and the input distance matrix are listed in Tables 2 and 3, respectively. Figure 6 depicts the tree for the first 10 strains on the list; Figure 7, the first 12 strains and Figure 8, the entire data set. The average percent standard deviations for the three trees are 10.3, 13.1, and 24.8, respectively. The same strains were used in the distance analysis shown in Figure 7 and the cladistic analysis in Figure 3. The two analyses illustrate different patterns of relationships that can be seen by comparing the

TABLE 3. Calculated distance matrix using Jaccard's coefficient subtracted from 100 to convert it to a distance measure.

	IIA1	2B3	NY1	HB1	SF1	UP1	ED1	MF2	I3	WR2	3B1	1B3	II A4	II A9	II A10	II A11	II A12
IIA1	--																
2B3	100	--															
NY1	20	80	--														
HB1	20	80	0	--													
SF1	30	30	30	30	--												
UP1	20	80	0	0	30	--											
ED1	20	80	10	10	40	10	--										
MF2	20	100	20	20	30	20	30	--									
I3	60	70	60	60	50	60	60	60	--								
WR2	50	80	50	50	40	50	50	50	40	--							
3B1	100	20	80	80	90	80	80	100	70	80	--						
1B3	20	100	20	20	30	20	30	20	40	50	100	--					
IIA4	100	20	80	80	90	80	80	100	70	80	20	100	--				
IIA9	50	60	70	70	80	70	70	70	80	80	90	70	80	--			
IIA10	100	20	80	80	90	80	80	100	60	50	80	20	80	80	--		
IIA11	20	80	0	0	30	0	10	20	60	50	80	20	80	70	80	--	
IIA12	100	20	80	80	90	80	80	100	70	80	20	100	0	80	0	80	--

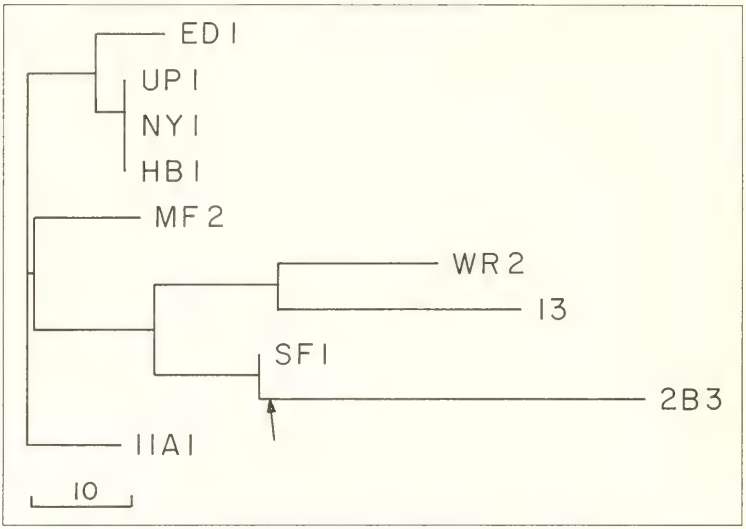


FIGURE 6. Distance tree obtained using the first 10 strains classified in Figure 3. The position of the midpoint root is designated by the arrow. Thescale bar represents 10 % divergence.

position of strain SF1 to the other strains. The difference in results is due to the calculation of distance coefficients compared to allelic distributions.

Figure 8 illustrates the addition of the first five strains isolated from the summer 1975 prebloom sample to the strains analyzed in Figure 7. Comparisons of Figures 6–8 illustrate the changes in topology among trees due to the addition of taxa. This can be illustrated by examining the relationship of strain SF1 in all three analyses. In Figure 6, it is the sister taxon to 2B3; in Figure 7, it is the sister to 2B3 and 3B1. In Figure 8, its position has shifted to a location basal to the branch leading to WR2 and I3. Comparisons of the tree distances between taxa also change with the addition of taxa. For example, the input distance from strain SF1 to strain 2B3 is 30 (Table 3). The tree distances are 38, 40, and 72 for figures 6–8, respectively. The input distance between SF1 and ED1 is 40. The tree distances are 46, 37, and 35, respectively, for the three analyses. The positions of the calculated midpoint roots for all three distance trees are shown. In all cases, the root falls between strain 2B3 and the next adjacent taxon, with strains isolated in the summer on both sides of the root.

Discussion

None of the analyses using single strains as terminal taxa recovered the seasonal patterns detected in the original analysis (Gallagher 1980). In both the cladistic and the distance analyses, the addition of taxa to the tree changed topologies among all of the taxa. This was an expected result. The pattern of relationships revealed by both cladistic and distance analyses is based on the overall fit of all of the taxa in the matrix to the analysis. Adding taxa changes the relationships.

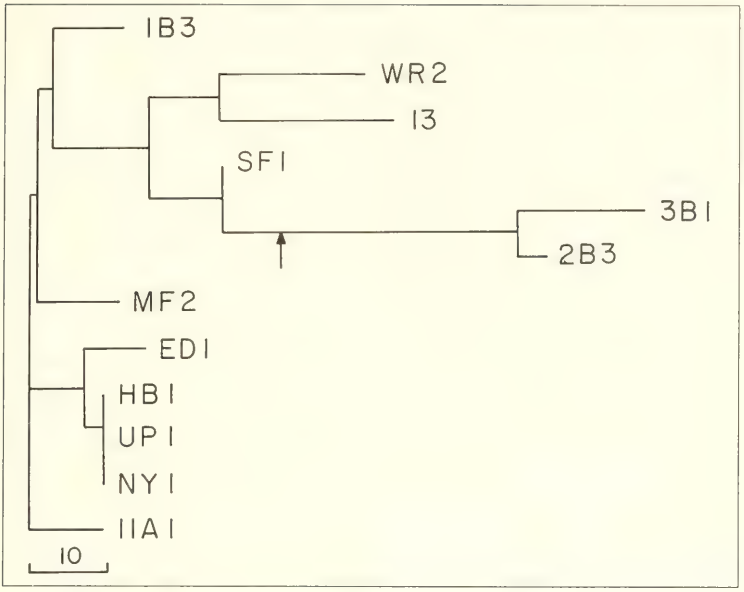


FIGURE 7. Distance tree obtained using all of the strains shown in Figure 3.

In the cladistic analysis, the increase in sample size was also associated with an decrease in the consistency index. The pattern of decreasing CIs with the addition of taxa to an analysis is common to all cladistic studies (Sanderson and Donoghue 1989). Above the species level, this phenomenon has been attributed to increased detection of parallelisms and convergences (homoplasy) in the data set (Sanderson and Donoghue 1989). Here, at the population level, increasing the number of strains increases the probability of detecting the reticulate relationships among characters caused by interbreeding. As was noted in Gallagher (1982), out of the 457 strains isolated in the Bay, 103 fell into the Mixed and Rare categories of strains that have common summer alleles at some loci and winter alleles at other loci. Another 41 strains fell into the Whet group that is heterozygous at one locus for some common winter alleles. Therefore, 32% of the strains isolated showed evidence of genetic introgression between the summer and winter extremes. Increasing the sample sizes improves the possibility of including these strains in a data matrix. A simple parsimony analysis results in unresolved consensus trees when strains are treated as terminal taxa because a large number of equally parsimonious trees are generated to account for the multiple associations of alleles at different loci. Each allele must evolve multiple times on different branches. This accounts for the increase in the detected homoplasy of the data set and the decline in CI with larger sample sizes. Successive weighting improves the resolution because it gives the characters that co-occur most frequently higher weights with each round of analysis until the tree stabilizes. Co-occurrence of characters at the population level is caused by linkage disequilibrium. This is the non-random association of particular alleles at some loci and alleles at other loci. In diatoms, the combination of asexual reproduction and sexual reproduction with the pos-

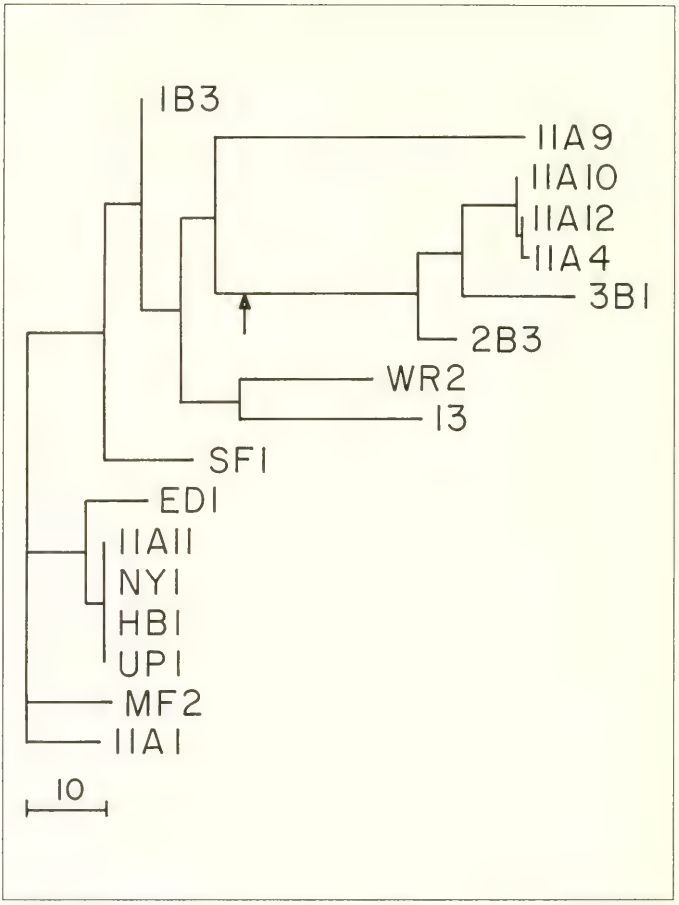


FIGURE 8. Distance tree obtained using all of the strains in Figure 7 plus the first five strains isloated in the summer prebloom of 1975.

sibility of both outbreeding and selfing can create linkage disequilibrium in three ways: (1) linkage on the same chromosome, (2) non-random association of gametes, and (3) differential asexual growth of different genotypes. Successive weighting is then able to resolve some of these groups. However, even though the differentiation among the common summer and winter forms is extreme, there is some heterogeneity within these groups. Locus TO1 has three common summer alleles and three different common winter alleles. The GDH locus is diverse at all times of year and no seasonal differences in frequencies are present. This intragroup diversity then causes the summer and winter groups to frag-

ment into different common subgroups when the strains and alleles are examined independently. This prevents resolution of clear seasonal patterns in the data set.

There is a disturbing aspect of these analyses. When very small numbers of strains are used in the analysis, the probability of identifying the reticulate nature of relationships is reduced. The cladograms based on these small sample sizes thus appear to be very well-supported relationships and appear to reveal patterns, and the addition of larger sample sizes gives the impression of confounding the relationships. In other words, it appears that increasing the sample size degrades the results rather than improves them. In fact, this is really not the case. Larger samples simply reveal the reticulate nature of the character distributions of *S. costatum* and support the conclusion that the summer and winter blooms are simply opposite extremes of a genetic continuum rather than separate species.

The problem of decreasing resolution with increasing sample size is not a problem with cladistics. Distance analyses also show decreasing resolution. Although it is not possible to calculate a distance tree with the PHYLIP program for all of the taxa, it is possible to run enough analyses to determine that adding taxa creates a "bushy" structure with calculated branch lengths that deviate from the lengths in the input distance matrix. Many branches with zero lengths are encountered as taxa are added and interpretation of pattern becomes increasingly more difficult. Distance trees suffer a disadvantage compared to cladistic analyses with successive weighting. A distance tree is based on pairwise calculation of distance coefficients and the allelic distributions are not used directly. For example, in Table 2, strains SF1 and WR2 have a distance coefficient of 0.40, as do strains I3 and 1B3, but each of these pairs of strains has different alleles. There is also no way to weight different branches. Although different distance coefficients exist that take into account frequencies of alleles at different loci, these coefficients are meant to be applied to populations, not individual genotypes as is used here. In any case, they all share the problem of discarding character information. Therefore, if the only way to resolve recurrent groups is to use linkage disequilibrium, then a distance analysis cannot succeed. An additional problem with distance trees is determination of a root. For many diatoms, determination of an outgroup is unclear. Some investigators have used a midpoint root as an alternative (e.g., Cembella et al. 1988). The validity of this assumption is based on equal amounts of divergence among branches of the tree. In the current analysis the position of the root is on a long branch and there is no reason to assume equal rates of evolution. No pattern is discernable because strains isolated in the summer occur on both extreme ends of the tree.

It has been suggested that the summer and winter populations of *S. costatum* be divided into different species based on the large genetic distance between them compared to higher organisms (Gallagher 1980). The current analysis shows that that conclusion is not supported by the allozyme data nor morphological differences (Gallagher, 1980). Large amounts of genetic diversity at the population-level have been reported for bacteria also (McArthur et al. 1988) and for other protist groups. Clearly, empirically derived coefficients of taxonomic divergence developed for higher organisms do not apply to unicellular ones.

Could the addition of more molecular characters improve the resolution of the tree and result in the division of the Narragansett Bay populations of *S. costatum* into different species or varieties? Potentially, they could. However, these characters would have to be chosen with caution. One of the strengths of enzyme electrophoresis is that it examines variation in the nuclear genome at randomly chosen loci. Many molecular techniques, such as sequencing, usually examine variation only at a single locus. At lower phylogenetic levels, particularly in the presence of linkage disequilibrium, patterns of variation in a

single gene can give a false impression of divergence. This has been termed the "gene tree vs. species tree" problem (Pamilo and Nei 1988). For example, consider the problem of examining variation in chloroplast DNA (cpDNA) as an additional set of characters. For most organisms, cpDNA is inherited uniparentally and is therefore not subject to recombination. This means that it behaves genetically as if it were a single gene. Therefore, the differences among cpDNA patterns obtained from different strains are estimates of the divergence in the chloroplast DNA lineages, and are not necessarily representative of the entire genome of the taxa in question. Consequently, the pattern of cpDNA differences must be evaluated relative to markers developed for nuclear genes in order to determine the true patterns of differences. A similar problem can be found for sequencing multicopy genes, such as 16s-like ribosomal DNA. These genes do not evolve independently, but evolve together in a process called concerted evolution (Appels and Honeycutt 1986). When a mutation is introduced in one of the copies of the gene, it can propagate through the other copies to homogenize the gene family. Similarly, heterogeneous copies of the gene that are combined in one genome as a result of mating genetically distinct individuals will eventually homogenize. The rate at which this homogenization process occurs is not known. Microheterogeneity among copies of 16s-like genes in a position that is highly conserved in other organisms was noted in one strain of *S. costatum* by Medlin et al. (1988) and could possibly be additional evidence for introgression. However, as concerted evolution progresses over time, the microheterogeneity at that site may be lost.

What recommendations can be made, then, for solutions for these problems? The first is to use groups of strains as the terminals. This approach is described in detail for the Narragansett Bay data set in a companion paper (Gallagher, in prep.). These groups need not be large enough to generate allele frequencies, presence/absence data for the groups seems to be sufficient and were used to generate the cladogram shown in Figure 1 (Gallagher, in prep). Estimates of the minimum number of strains per group could be determined by a simulation based on resampling the *S. costatum* data set at random to attempt to recover the seasonal patterns. For other analyses, the characteristics of the groups could be defined by hypotheses of relationships, i.e., for a study of morphological divergence groups should be composed of strains with different morphologies. For a biogeographical study, groups of strains from different regions could be compared. For all of these studies a cladistic approach to the data will have the greatest utility because it has the best methodological and philosophical foundation for incorporating different types of data into a single analysis or series of related analyses.

In order to optimize a sampling strategy for labor intensive molecular analyses, a hierarchical approach of using low resolution methods with larger sample sizes to determine sample sizes for higher resolution techniques can be taken. For example, the pattern of restriction fragment polymorphisms for a larger sample size can be used to select strains for more intensive sequencing studies.

It is necessary that phycologists work together to generate enough data sets so that potential benchmarks for species-level and population-level amounts and patterns of molecular divergence for different algal groups can be developed. It is clear that empirical benchmarks developed for higher organisms do not apply to microalgae. For example, in higher plants, chloroplast DNA (cpDNA) rflps usually vary only at the generic level. In diatoms, they vary at the population level (Stabile et al. 1990).

Finally, diatomists need to develop a molecular equivalent of type specimens. One of the great challenges of molecular biology is that new techniques are being developed at a rapid pace. It is extremely difficult to relate the characters used by different studies to each other without applying them to the same set of specimens. Therefore, wherever

possible it is desirable to include universally available strains in an analysis to provide reference points. Many of these strains can be obtained from the various worldwide culture collections. Strains can also be deposited in the collections. When this is not possible, it is recommended that DNA from the strains be saved for analysis by others. It is hoped that these recommendations would simply make the philosophy and approaches taken to molecular data more similar to that taken to morphological data.

Acknowledgements

This study was supported, in part, by National Science Foundation grants DEB80-21744 and OCE-8809484 and by PSC-CUNY grants 665155 and 669175 from the Research Foundation of the City University of New York. Bruce Huber helped with PHYLIP, read the manuscript, and provided valuable comments.

Literature Cited

APPELS, R. AND R. L. HONEYCUTT. 1986. rDNA: Evolution over a billion years. Pp. 81–137 *in* DNA Systematics, S. K. Dutta, ed. CRC Press. Boca Raton.

AVISE, J. C. 1975. Systematic value of electrophoretic data. Syst. Zool. 23:465–481.

BRAND, L. E. 1990. Review of genetic variation in marine phytoplankton species and the ecological implications. Biol. Oceanogr. 27:236–245.

BUTH, D. G. 1984. The application of electrophoretic data in systematic studies. Ann. Rev. Syst. Ecol. 15:501–522.

CEMBELLA, A. D., F. J. R. TAYLOR, AND J. C. THERRIAULT. 1988. Cladistic analysis of the electrophoretic variants within the toxic dinoflagellate genus Protogonyaulax. Bot. Mar. 31:39–51.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

———. 1988. Hennig86 Reference. Version 1.5.

———. 1989. The retention index and the rescaled consistency index. Cladistics 5:417–420.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

FERGUSON, A. 1988. Isozyme studies and their interpretation. Pp. 184–201 *in* Prospects in Systematics, D. L. Hawksworth, ed. Systematics Association, Clarendon Press, London.

FITCH, W. M. AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. Science 155:279–284.

GALLAGHER, J. C. 1979. Population genetics of *Skeletonema costatum* in Narragansett Bay. Ph.D. thesis. U. Rhode Island. 232 pp.

———. 1980. Population genetics of *Skeletonema costatum* in Narragansett Bay. J. Phycol. 16:464–474.

———. 1982. Physiological variation and electrophoretic banding patterns of genetically different seasonal populations of *Skeletonema costatum* (Bacillariophyceae). J. Phycol. 18:148–162.

———. 1986. Population genetics of microalgae. *In* Algal Biomass Technologies: An Interdisciplinary Perspective, W. R. Barclay and R. P. McIntosh, eds. Nova Hedwigia 83:6–14.

———. Genetic structure of microalgal populations. II. Time-space interactions in *Skeletonema costatum* (Bacillariophyta) in Narragansett Bay, R. I. (submitted).

GUILLARD, R. R. L. AND J. H. RYTHER. 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can. J. Microbiol. 8:229–239.

HAYHOME, B. A. AND L. A. PFIESTER. 1983. Electrophoretic analysis of soluble enzymes in five freshwater dinoflagellate species. Am. J. Bot. 70:1,165–1,172.

HAYHOME, B. A., D. M. ANDERSON, D. M. KULIS, AND D. J. WHITTEN. 1989. Variation among congeneric dinoflagellates from the northeastern United States and Canada. Mar. Biol. 101:427–435.

LOVELESS, M. D. AND J. L. HAMRICK. 1984. Ecological determinants of genetic structure in plant populations. Ann. Rev. Syst. Ecol. 15:65–95.

MCARTHUR, J. V., D. A. KOVACIC, AND M. H. SMITH. 1988. Genetic diversity in natural populations of a soil bacterium across a landscape gradient. Proc. Nat. Acad. Sci. 85:9621–9624.

MEDLIN, L. K., H. J. ELWOOD, S. STICKEL, AND M. L. SOGIN. 1988. The characterization of enzymatically amplified eukayotic 16S-like rRNA-coding regions. Gene 71:491–499.

MICKEVICH, M. F. AND M. S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool. 25:260–270.

MICKEVICH, M. F. AND C. MITTER. 1983. Evolutionary patterns in allozyme data: a systematic approach. Pp. 169–176 *in* Advances in Cladistics, Vol. 2. Proceedings of the 2nd Meeting of the Willi Hennig Society, N. I. Platnick and V. A. Funk, eds. Columbia U. Press. New York.

OLSEN, J. L. 1990. Nucleic acids in algal systematics. J. Phycol. 26:209–14.

PAMILO, R. AND M. NEI. 1988. Relationships between gene trees and species trees. Molec. Biol. Evol. 5:568–583.

SNEATH, P. H. H. AND R. R. SOKOL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco.

SANDERSON, M. J. AND M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution 43:1781–1795.

SOUDEK, D. AND G. G. C. ROBINSON. 1983. Electrophoretic analysis of the species and population structure of the diatom *Asterionella formosa*. Can. J. Bot. 61: 418–433.

STABILE, J. E., J. C. GALLAGHER, AND E. T. WURTZEL. 1990. Molecular analysis of intraspecific variation in the marine diatom *Skeletonema costatum*. Biochem. Syst. Ecol. 18:5–9.

WOOD, A. M. 1987. Molecular biology, single cell analysis and quantitative genetics:new evolutionary genetic approaches in phytoplankton ecology. Pp. 41–71 *in* Immunochemical Approaches to Estuarine, Coastal and Oceanographic Questions. C .M. Yentsch, F. C. Mague, and P. K. Horan, eds. Elsevier. New York

Mathematical Modeling of Silicoflagellate Skeletal Morphology and Implications Concerning Skeletal Latticeworks

by

K. McCartney

University of Maine at Presque Isle, Presque Isle, Maine 04769

J. Ernissee

Department of Geology and Geography, Clarion University, Clarion, Pennsylvania 16214

and

D. E. Loper

Geophysical Fluid Dynamics Institute, Florida State University, Tallahassee, Florida 32306

with 3 figures

Abstract: Silicoflagellates are one of three siliceous microfossil groups that have skeletons made up of a rigid latticework of rods. Mathematical modeling of silicoflagellate skeletal design suggests that an important factor influencing skeletal shape is the minimization of apical surface area, while the reduction of skeletal material appears to have secondary importance. Presumably, minimization of area is also important for the radiolarians and ebridians, which are the other groups having latticework skeletons. The reason why these three groups use such a skeletal design, and why this morphology is not found among non-siliceous groups, remains a mystery.

Introduction To Latticework Skeletons

A wide variety of different skeletal types are used in the organic world (see Rief and Thomas 1975). Skeletal latticeworks, in which linear or curved rods are interconnected to form a rigid net that encloses most of the organism, are among the less common, being used only by the radiolarians, ebridians, and silicoflagellates. These microorganisms are siliceous and planktic; indeed, the only group of siliceous organisms that do not have

latticework skeletons are the diatoms. Rigid latticeworks are not found among macroorganisms or microorganisms that are benthic or have calcareous skeletons.

The precise function of the latticework skeleton is enigmatic, but the occurrence of latticeworks among three distinctly different organism groups suggests some functional convergence. Latticework skeletons have obvious advantages and disadvantages over those skeletons that have continuous or overlapping surfaces that surround most of the cell, such as found in foraminifera, coccoliths, and diatoms. The most obvious advantage of the skeletal latticework is its light weight, an important attribute for organisms that must remain in suspension. Use of geodesic domes in building design suggests that rigid latticeworks offer considerable strength for less weight, although no research has been done on the strength of latticeworks in the context of organisms or on the reasons why such microorganisms might need strong skeletons. The large openings between the skeletal elements suggest that the skeleton would not serve well as a defense against predators.

McCartney and Loper (1989) have proposed three reasons why skeletal latticeworks are found exclusively among siliceous rather than carbonate organisms: (1) the tensile strength of quartz is higher than that of calcite, which may offer advantages for skeletal latticeworks; (2) the greater surface area of the latticework skeleton may not favor calcite, which dissolves more easily in seawater than does silica; and (3) since silica is undersaturated in modern oceans, siliceous organism prefer latticeworks because they use less skeletal material than skeletons that surround the organism with continuous surfaces. Together these reasons suggest that latticework skeletons offer a lightweight construction for which silica is the best suited material available to the organism.

Mathematical Modeling of Latticework Skeletons

Mathematical models of silicoflagellate skeletal morphologies have recently been constructed in order to learn more about skeletal latticeworks and determine factors influencing silicoflagellate skeletal design. Silicoflagellates are ideal for preliminary modeling of this type because their simple geometric designs and lack of internal skeletal elements make the mathematical modeling of the three-dimensional framework much easier than for more complex organisms, such as radiolarians. In addition, presence of a basal ring in silicoflagellates provides an easy basis for orienting the skeleton and provides a flat basal surface to further facilitate construction of mathematical models.

Models of silicoflagellate morphology reviewed here are based on optimization mathematics, in which one dependent variable is minimized over all possible values on one or more independent variables subject to certain constraints. Optimization morphologies are found throughout nature and are commonly seen as polygonal patterns such as the colonial structure of corals, the venation of the insect wing, or the cracks produced by the desiccation of mud. These patterns are the result of close-packing conditions and are efficient because the material needed for the walls between individual "cells" is minimized while still allowing the volume of within each polygon to be relatively large.

The latticework skeletons of siliceous microorganisms have many characteristics similar to the polygonal structures above, including intersections formed by the juncture of three skeletal elements with angles commonly close to 120 degrees. However, the skeletal latticework is not the result of close-packing since the siliceous microorganisms are not colonial and the polygons formed by these elements are not the surface expression of planar structures that run through the organism. Indeed, latticework skeletons found among siliceous microorganisms differ considerably from the structures mentioned previously in that they are forms of intersecting rods rather than planes.

That latticework skeletons tend to have a spherical shape suggests that they result from area minimization. This has been previously proposed for some radiolarian skeletons (Thompson 1942; Almgren 1982), and considerable optimization study has been done with soap bubbles (see Almgren and Taylor 1976). A surface of minimal area results when some physical effect, such as surface tension, acts to minimize the area of the surface given some constraint, such as constant enclosed volume. The sphere is the minimum surface enclosing a specified volume, provided that no other constraints apply.

Silicoflagellates, however, differ from radiolarians and ebridians in their relatively large and flat basal area, which gives hemispherical rather than spherical shape to the skeleton. The basal opening is also undivided so that it is much larger than any of the apical openings. The differences between apical and basal surfaces strongly suggest that these surfaces play different roles, that the silicoflagellate skeleton is not the result of simple minimization of total area, and that area minimization applies to the apical surface. Presence of paired silicoflagellates with connected basal rings suggests that the basal surface is important to the reproduction of the organism.

The general morphology of silicoflagellate skeletons suggests that two factors influence skeletal design. The hemispherical shape of the apical surface indicates that reduction of apical surface area is an important factor while the simple skeletal morphologies suggest that reduction of skeletal material is also important. Neither of these, however, are expected to be important to the exclusion of all others; silicoflagellate skeletons are probably a compromise between these and other factors. If the minimization of apical surface area was all-important, then the silicoflagellate would have a more radiolarian appearance, with many skeletal elements and smaller open spaces so that apical structure would closely approximate a spherical surface. If the reduction of skeletal material was the all-important factor then the skeleton would be of extremely simple shapes, if indeed it had a skeleton at all.

Modeling of Silicoflagellate Morphology

In modeling silicoflagellate morphologies through optimization mathematics we seek to construct formulae that minimize one variable with respect to others and to determine the shape of the resulting skeletal design. Four external variables are of special interest, these being the apical surface area (A_a), the basal surface area (A_b), the volume (V) enclosed between these surfaces, and the total length (S) of the skeletal elements. Because four variables are difficult to present mathematically and graphically, we have reduced these to three variables by dividing the basal area into each of the others to produce the dimensionless variables A*, V*, and S* (see McCartney and Loper 1989, for formulae). Dimensionless variables have the additional advantage of being unitless.

The apical area is determined by dividing the apical surface into triangular facets (see McCartney 1988a, b) and summing their total area. The volume is measured by computing the area between each triangular facet and the plane of the basal ring, and summing this total. The procedure used for modeling silicoflagellate morphology is to optimize a single dependent variable with respect to V*, within the skeleton. Formulae have been derived (see McCartney and Loper 1989) that minimize A* or S*; these formulae were constructed to include a number on independent, dimensionless, variables from which we could figure the shape of the optimal morphology. Examples of internal variables include length of the apical bridge and shape of the apical and basal rings. These internal variables are allowed to vary to optimal values, for the internal variables can be specified if we wish to study a particular shape, or see how other variables change if one variable is specified.

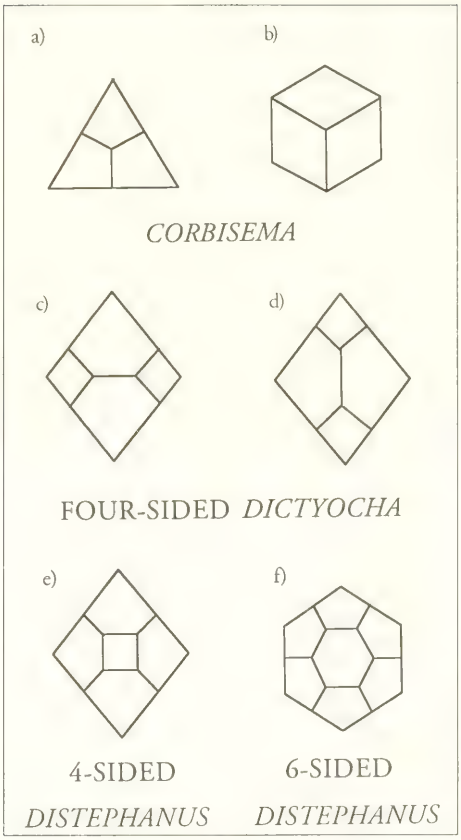


FIGURE 1. Silicoflagellate skeletal morphologies as modeled by optimization mathematics: a) *Corbisema* with straight basal sides, b) *Corbisema* with bowed sides, c) *Dictyocha* with bridge parallel to minor axis, d) *Dictyocha* with bridge parallel to major axis, e) four-sided *Distephanus*, f) six-sided *Distephanus*.

Optimization models for four basic silicoflagellate skeletal morphologies have been constructed. The four studied morphologies (Fig. 1) are the three-sided *Corbisema*, the four-sided *Dictyocha*, and the four- and six-sided *Distephanus*. The internal variables within each model were varied in order to produce a wide variety of forms within each group, such as *Dictyocha* with apical bridge parallel to the long or short axis (Figs. 1c, d, respectively), or *Corbisema* with bowed sides (Fig. 1b). Thus, different silicoflagellate configurations can be modeled and compared to determine their efficiency at reducing A* or S* for given V*.

We have found that for each of the four models, minimization of apical surface area (A*) consistently produce easily recognizable silicoflagellate configurations, while minimization of skeletal material (S*) commonly results in configurations that are rare or not found in silicoflagellates. We (McCartney and Loper 1989) conclude that silicoflagellate skeletons

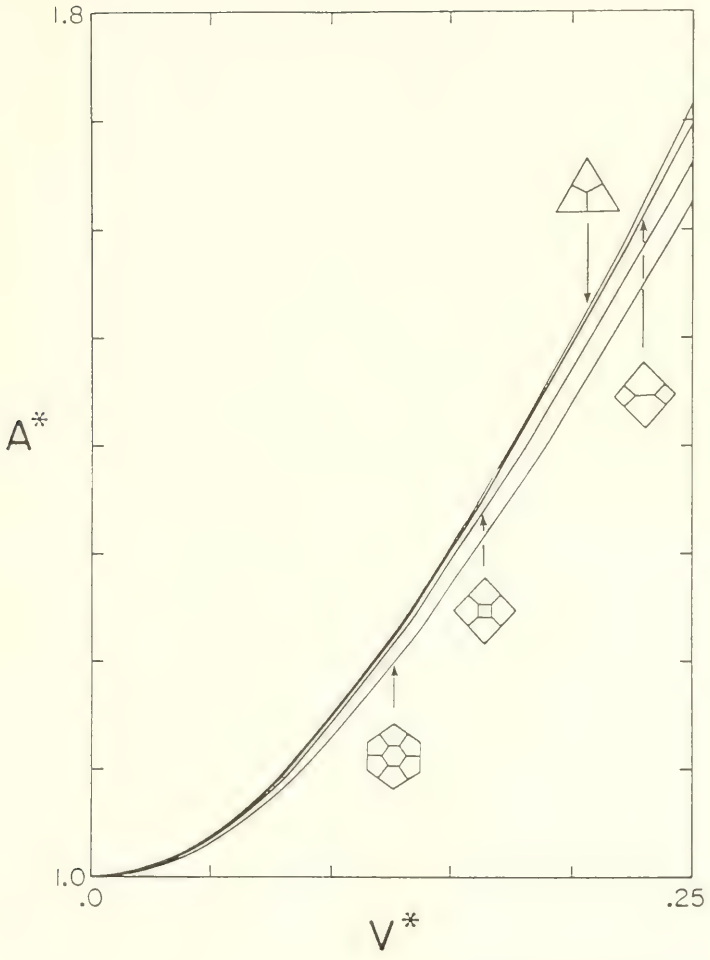


FIGURE 2. Plot showing A* values for given V* for four silicoflagellate morphotypes. The six-sided *Distephanus* morphology has the lowest A* values of those tested.

tend to reduce the apical surface area to a minimum and that this factor is more important than reduction of skeletal material. However, comparison between models shows that some silicoflagellate designs are more efficient at minimizing A* than others. Morphologies with a greater number of basal sides and more complex apical structures minimize A* better than simpler skeletal designs. For the four silicoflagellate groups modeled thus far, the six-sided *Distephanus* best minimizes A* while the three-sided *Corbisema* has the highest A* values (Fig. 2).

The occurrence of relatively simple silicoflagellate skeletal configurations such as *Corbisema* suggest that other factors besides the minimization of A* are also important to the organism. A strong candidate for a second factor, as mentioned previously, is the reduction of skeletal material. Silica is undersaturated in the oceans and may be a limiting nutrient to silicoflagellates (Tappan 1980). Reduction of skeletal material also reduces the weight of the skeleton and, thus, settling velocity. S* values for silicoflagellate configurations that minimize A* are shown in Figure 3. The simpler morphologies utilize less skeletal material for all values of V*.

The simple morphology of *Corbisema* lends itself to a more detailed model (McCartney and Loper, 1992) in which the basal sides can be bowed outwards. Tests of this model show that the most efficient *Corbisema* morphology for minimizing A* has basal sides that bow outwards so that the ring itself would be round (see Fig. 1b), while the morphology that uses least skeletal material has sides that bow outwards to a lesser degree. The morphologies that have less skeletal material are more typical of fossil *Corbisema* skeletons, suggesting again that silicoflagellate skeletal material is an important factor. These data support the idea that silicoflagellate skeletal morphology is a compromise between reduction of skeletal material and reduction of apical surface area.

Discussion

Perhaps the most important conclusion resulting from the optimization modeling of silicoflagellates is the apparent importance of apical surface area. McCartney and Loper (1989) have presented several hypotheses for why this is important and believe that the most reasonable answer is that silicoflagellates minimize apical surface area in order to minimize surface energy. This conclusion suggests that surface tension plays a very important role for the silicoflagellate organism. Unfortunately, there is very little literature on the relationship between surface energy and organisms, particularly those of very small size, and this hypothesis remains to be tested.

The importance of minimizing apical surface area should also apply to radiolarians and ebridians. The skeletons of these organisms, however, have internal elements and lack the basal ring that gives a hemispherical shape to the skeletons of silicoflagellates. Whether these differences are caused by some functional adaptation or simply reflect differences in growth processes or evolutionary history is one of many questions that remain unanswered. That the most abundant and diverse group of siliceous organisms, the diatoms, use a completely different skeletal design suggests that the reduction of silica usage may be less important or that defense against predators is more important with the diatoms than with the other siliceous groups.

The geographic distribution of silicoflagellate skeletal morphologies is interesting in that, throughout the Cenozoic, more complex morphologies are found at higher latitudes while simpler morphologies are found at lower ones. For example, six-sided *Distephanus* predominate at high latitudes in modern oceans while four-sided *Dictyocha* predominate at lower latitudes. In the Paleogene *Dictyocha* predominated at high latitudes while *Cor-*

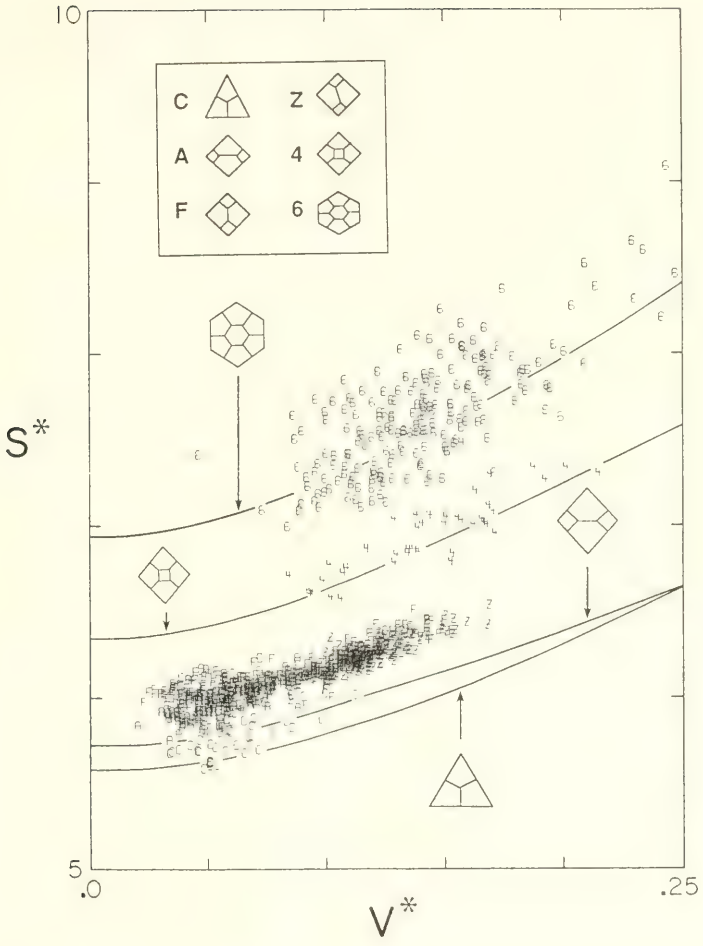


FIGURE 3. Plot showing V* versus S* for the four silicoflagellate morphotypes. The S* values are obtained for a morphology with minimum A*. For any value of V*, the six-sided *Distepahnus* uses the most silica while the four-sided *Dictyocha* uses the least. The numbers and letters shown in the inset represent measured silicoflagellate specimens. A = *Dictyocha* with bridge parallel to minor axis. F = *Dictyocha* with bridge parallel to major axis. Z = *Dictyocha* with diagonal bridge. C = *Corbisema*. Numbers indicate a *Distephanus* with that number of basal sides. From McCartney (1988a).

bisema were more common at lower ones. This suggests that the minimization of apical surface might be more important in colder waters than near the equator, while the importance of reducing skeletal material increases towards the equator. Thus, there might exist environmental reasons that influence each of these factors, and silicoflagellate morphology in general.

Acknowledgements

We gratefully acknowledge assistance, constructive comments, and suggestions made by R. D. K. Thomas and financial support from the Division of Math/Science, University of Maine at Presque Isle. This is Contribution No. 343 of the Geophysical Fluid Dynamics Institute, Florida State University, Florida State University, Tallahassee, FL 32306.

Literature Cited

ALMGREN, F. J., JR. 1982. Minimal surface forms. Mathematical Intelligencer 4:164–172.

ALMGREN, F. J., JR. AND J. E. TAYLOR. 1976. The geometry of soap films and soap bubbles. Sci. Am. 235:82–93.

MCCARTNEY, K. 1988a. Modeling silicoflagellate skeletal morphology. Ph.D. Dissertation, Florida State University, Tallahassee. 217 pp.

———. 1988b. SILICO: A computer program for the three-dimensional measurement of silicoflagellate skeletons. Computers & Geosciences 14:99–111.

MCCARTNEY, K. AND D. E. LOPER. 1989. Optimization of the silicoflagellate genera *Dictyocha* and *Distephanus*. Paleobiology 15:283–298.

———. 1992. Optimization modeling of the silicoflagellate genus *Corbisema*. Micropaleontology 38:87–93.

REIF, W-E. AND J. A. ROBINSON. 1975. Geometrical relationships and the form-function complex: animal skeletons. Neues Jahrb. Geol. Paleont. Monats. 3:184–191.

TAPPAN, H. 1980. The Paleobiology of Plant Protists. W. H. Freeman & Co., San Francisco. 1028 pp.

THOMPSON, D. W. 1942. On Growth and Form. Cambridge University Press (2nd ed.), Cambridge, England. 1116 pp.

Silica Content of Freshwater and Marine Benthic Diatoms

by

Daniel J. Conley

Horn Point Environmental Laboratory,
Center for Environmental and Estuarine Studies,
University of Maryland System, P. O. Box 775,
Cambridge, Maryland 21613

Paul V. Zimba

Department of Fisheries and Aquatic Science,
University of Florida Gainesville, Florida 32606

and

Edward Theriot

Academy of Natural Sciences of Philadelphia,
19th and The Parkway, Philadelphia, Pennsylvania 19103

with 1 figure and 2 tables

Abstract: The silica content of benthic diatoms was determined from cultures of 12 freshwater and six marine clones. Marine benthic diatom silica content per unit of biovolume (0.0199 + 0.0301 pmol μm^{-3}) was similar on average to that obtained for freshwater benthic diatoms (0.0179 + 0.0256 pmol μm^{-3}) and marine benthic diatoms contained on average significantly more silica per unit of biovolume than marine planktonic species (0.000502 + 0.000466 pmol μm^{-3}, Conley et al. 1989). Although limited, our data demonstrate that marine benthic diatoms can be as heavily silicified as freshwater benthic and planktonic diatoms. Therefore, differences in silica content per unit of biovolume between marine planktonic diatoms and other diatoms cannot necessarily be solely attributed to salinity. Our results coupled with a reported reduction in the silica content of marine diatoms from the geologic record implies that evolutionary changes have occurred in marine planktonic diatom silica content. We conclude that marine planktonic diatoms probably have reduced their silica content downward and have evolved to species that are better adapted to ambient environmental conditions as dissolved silica concentrations have decreased in the world's oceans.

By contrast, benthic diatoms are able to remain heavily silicified without losing a competitive advantage to more lightly silicified diatoms.

Introduction

Diatoms are known to adjust their silica content for a variety of reasons including growth rate, nutrient limitation, salinity, and temperature. A recent analysis that examined the silica content of diatoms as it related to cell size demonstrated that the amount of silica contained in the frustule of a planktonic diatom could be predicted from the biovolume of the diatom (Conley et al. 1989). Furthermore, Conley et al. (1989) have shown that freshwater planktonic diatoms have one order of magnitude more silica contained within the frustule per unit of biovolume than do marine planktonic species. Significant differences were not observed between freshwater pennate and freshwater centric diatom silica content when corrected for biovolume.

Casual observation has suggested that benthic diatoms are more heavily silicified than their planktonic counterparts. In this paper we will compare the silica content of marine and freshwater benthic diatoms to those determined for planktonic diatoms in a previous study (Conley et al. 1989) and address the question of whether the silica content of freshwater benthic diatoms are different from marine benthic diatoms. In addition, we will evaluate observed differences in diatom silica content in the context of the evolution of diatoms.

Materials and Methods

Twelve clones of freshwater benthic diatoms and six clones of marine benthic diatoms were grown in batch culture. Cultures were grown at 20° C and 100 μEinsteins m^{-2} s^{-1} illumination on a 16:8 L/D cycle. Diatoms were harvested during mid-exponential log-phase for determination of silica content, cell biovolume, and abundance. Freshwater diatom cultures were obtained from the Diatom Culture Collection of Loras College's Department of Biology (Czarnecki 1987), and isolates from Lake Lochlossa and Lake Okeechobee, Florida. Taxa used from the Loras College Diatom Collection included *Cocconeis placentula* var. *lineata* (Ehrenberg) V. H., *Cymbella minuta* Hilse ex Rabh., *Gophonema acuminatum* v. *pusilla* Grun., *Navicula cryptocephala* Kütz., *Nitzschia sigma* (Kütz.) W. Sm., *Pinnularia viridis* (Nitz.) Ehrenberg, and *Surirella ovata* Kütz. Taxa isolated from Lake Okeechobee included *Achnanthes* c.f. *minutissima* Kütz., *Navicula* c.f. *menisculus*, *Nitzschia palea* (Kütz.) W. Sm, and *Nitzschia subacicularis* (Hustedt) and *Achnanthes* c.f. *minutissima* Kütz. was isolated from Lake Lochlossa. The freshwater benthic diatom cultures were grown in volcanic ash media (Czarnecki 1987) and Woods Hole MBL media (Stein 1973).

Marine diatom cultures were obtained from the Provasoli-Guillard Center for Culture of Marine Phytoplankton, Bigelow Laboratory for the Ocean Sciences, West Boothbay Harbor, Maine. Species analyzed included *Achnanthes brevipes* (Ag.) Cl., *Amphiprora paludosa* v. *duplex* Donkin, *Amphora* sp., *Nitzschia frustulum* (Kütz.) Grun., *Stauroneis amphoroides* Grun, and an unidentified pennate diatom. The marine benthic diatom cultures were grown in f/2 media (Stein 1973). All clonal designations are reported in Tables 1 and 2.

Diatom silica content was determined by filtering replicate subsamples (30–50 mL) from cultures onto Nuclepore polycarbonate membrane filters (47 mm diameter, 0.4 μm porosity) at vacuum pressures less than 100 mm Hg. Filters were digested using a wet alkaline extraction (0.1 N NaOH) in a boiling water bath, neutralized, and the extract

measured for dissolved silica on a Technicon AutoAnalyzer II (Paasche 1980a; Krausse et al. 1983). Dissolved silica also was determined on the filtrates to ensure that cultures were silica sufficient. Silica content values determined in this study, therefore, contain both frustule and intracellular silica. However, the cell wall accounts for the majority of the silica measured from a cell (Werner 1977) with < 10 % of the silica retained on the filter as intracellular silica (Paasche 1980b; Taylor 1985).

Subsamples also were collected for cell density and biovolume measurements. Cell counts were made using the Utermohl sedimentation method as modified by Venrick (1978). Biovolume was determined by measuring 10 cells per culture and relating the taxa to specific geometric shapes. All statistical analysis was carried out using Statistical Analysis System for Personal Computers (SAS-PC).

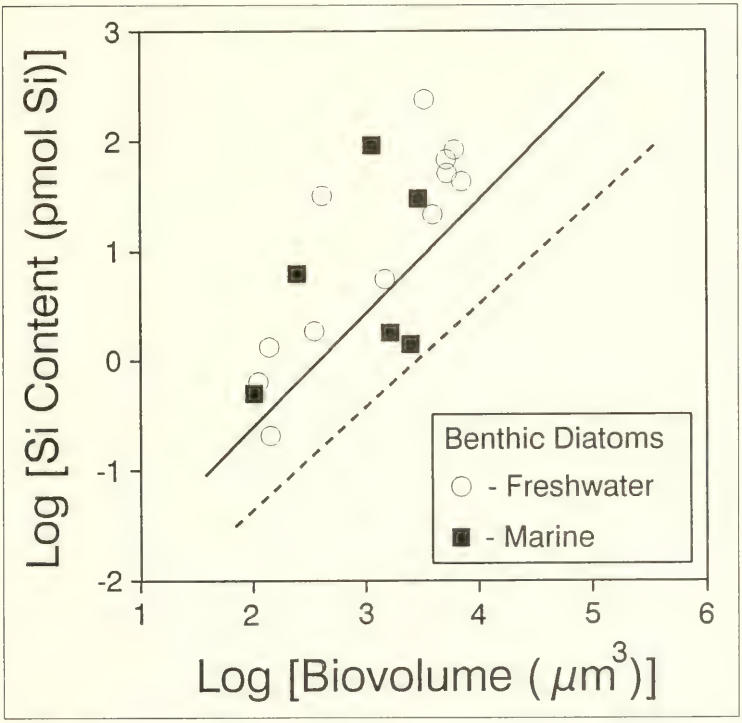


FIGURE 1. Relationship of biovolume to silica content of freshwater benthic diatoms (open circles) and marine benthic diatoms (closed squares). The regression lines are from freshwater planktonic diatoms (solid line) and marine planktonic diatoms (dashed line) determined in Conley et al. (1989).

TABLE 1. Silica content (pmol cell^{-1}) reported with standard deviation, biovolume (μm^3), and silica content per unit of biovolume (pmol μm^{-3}) of freshwater benthic diatoms.

Species	Clone	Silica content	Biovolume	Si/Biovolume
Achnanthes c.f. *minutissima*	OKEE	0.595 ± 0.564 (n=2)	112	0.00531
Achnanthes c.f. *minutissima*	LOCH	0.207 ± 0.204 (n=2)	144	0.00144
Cocconeis placentula v. *lineata*	A-83	233	3400	0.0685
Cymbella minuta	023	31.8	420	0.0757
Gomphonema acuminatum v. *pusilla*	A-67	81.3 ± 78.8 (n=2)	6210	0.0131
Navicula cryptocephala	38/03/A	42.8	7220	0.00593
Navicula c.f. *menisculus*	OKEE	1.30 ± 0.310 (n=2)	144	0.00903
Nitzschia palea	OKEE	1.67 ± 1.19 (n=2)	358	0.00467
Nitzschia sigma	L-7	66.3	5100	0.0130
Nitzschia subacicularis	OKEE	5.58 ± 2.29 (n=2)	1490	0.00375
Pinnularia viridis	A-53	50.2 ± 44.5 (n=2)	5395	0.00930
Surirella ovata	A-55	21.2 ± 18.8 (n=2)	4000	0.00530

Results

The silica content of both freshwater benthic diatoms (Table 1) and marine benthic diatoms (Table 2) varied by about a factor of two within clones harvested on different dates; silica content has been reported to vary by an order of magnitude within a single clone (Taylor 1985). Reproducibility in benthic diatoms is more problematic than in planktonic diatoms because benthic diatoms often clump together and adhere to the culture vessel wall.

The amount of silica per unit of biovolume in marine benthic diatoms averaged 0.0199 ± 0.0301 pmol μm^{-3} and is several orders of magnitude greater than determined for marine planktonic species (0.000502 ± 0.000466 pmol μm^{-3}, Conley et al. 1989). The amount of silica per unit of biovolume in marine benthic diatoms also was similar on average to those obtained from freshwater benthic diatom cultures (0.0179 ± 0.0256 pmol μm^{-3}). For the most part, freshwater benthic diatoms contained a similar amount of silica per unit of biovolume as their planktonic counterparts (Fig. 1), although two (*Cocconeis placentula* v. *lineata* and *Cymbella minuta*) of the 12 diatom species analyzed contained significantly more silica per unit of biovolume than the others ($p < 0.0001$). A significant log-log linear relationship was obtained between freshwater benthic diatom silica content and biovolume ($r^2 = 0.76$, $p < 0.0002$, $n = 12$):

$$\log_{10}[\text{silica content (pmol cell}^{-1})] =$$

$$(1.18, \text{S. E.} = 0.210)\log_{10}[\text{biovolume } (\mu m^3)] - (2.60, \text{S. E.} = 0.662). \quad (1)$$

TABLE 2. Silica content (pmol cell $^{-1}$) reported with standard deviation, biovolume (μm^3), and silica content per unit of biovolume (pmol μm^{-3}) of marine benthic diatoms.

Species	Clone	Silica Content	Biovolume	Si/Biovolume
Achnanthes brevipes	WAT7	1.76	1680	0.00105
Amphiprora paludosa v. *duplex*	73M	90.6 ± 116 (n=4)	1152	0.0786
Amphora sp.	WTAM	6.16	252	0.0244
Nitzschia frustulum	13M	0.504 ± 0.271 (n=3)	108	0.00467
Stauroneis amphoroides	11M	30.0 ± 50.3 (n=4)	2956	0.0101
Unidentified pennate	WTMB	1.42	2518	0.000654

This relationship was not significantly different from that obtained for freshwater planktonic diatoms by Conley et al. (1989). A significant relationship was not obtained between marine benthic diatom silica content and biovolume ($r^2 = 0.16$, $p < 0.44$, $n = 6$).

Discussion

Our results demonstrate that benthic diatoms generally contain significantly more silica per unit of biovolume than do planktonic diatom species and that marine benthic diatoms can be as heavily silicified as freshwater benthic diatoms. Salinity differences between the two environments cannot account for the variation observed in silicification between marine and freshwater planktonic diatoms (Conley et al. 1989). Previous research on the effects of salinity on diatom silica content are equivocal. Olsen and Paache (1986) found that cells of *Thalassiosira pseudonana* had a higher silica content at lower salinities. Conversely, McMillan and Johansen (1988) found that valves of *T. decipiens* were less heavily silicified at lower salinities.

The leading hypotheses as to why freshwater planktonic diatoms contain relatively more silica than marine planktonic diatoms relate to differences in sinking strategy and differences in ambient dissolved silica concentrations between freshwater and marine environments, factors that generally are not a concern in the ecology of benthic diatoms. It is interesting to note that the more lightly silicified benthic species often are observed in plankton samples. For example, two of more lightly silicified marine diatoms, *Achnanthes brevipes* and *Nitzschia frustulum*, are both species commonly found in the plankton of Chesapeake Bay (Wilderman 1984). In freshwaters, many planktonic diatoms are tychoplanktonic and spend a portion of their life cycle in the benthos, often in resting stages, such that there are very few true freshwater diatoms that spend their entire life history in a planktonic phase. For marine planktonic species it may be an advantage to have a lower silica content, making it less likely to sink out of the photic zone, since, in the oceans, once a diatom is lost from the upper mixed layer reentry into the photic zone is difficult.

Relative dissolved silica availability between marine and freshwaters also might select for more lightly silicified marine planktonic diatoms. In general, there is a connection between silicification and ambient dissolved silica concentrations (Paasche 1980b), which

might explain the differences in silicification between marine planktonic diatoms and other diatoms. Although freshwaters may have low dissolved silica concentrations (usually during summer), dissolved silica concentrations are often well above limiting values during the seasons of optimal growth. By contrast, dissolved silica concentrations in most regions of the world oceans are extremely low, except in polar waters where the most heavily silicified marine diatoms are found.

Differences in the amount of silica per unit of biovolume in marine planktonic diatoms support the assertion that the silica content of marine planktonic diatoms has been reduced with time. Barron and Baldauf (1989) suggest that Paleogene (65–23 Ma) marine diatoms and radiolarians appear to possess considerably thicker-walled siliceous frustules and tests than their Neogene (23 Ma–present) counterparts. Moore (1969) reported that Quaternary radiolarians have one-fourth less silica than Eocene radiolarians and that radiolarian silica content has linearly decreased downward from 50 Ma to present. Barron and Baldauf (1989) suggest that a substantial evolutionary turnover occurred in marine diatoms and radiolarians during the early Oligocene as relative dissolved silica availability changed in the paleo-oceans. The changes in silica content may reflect an increased competition for dissolved silica during the late Cenozoic leading to more lightly silicified furstules in Neogene diatoms. Prior to the evolution of organisms requiring dissolved silica for growth, concentrations in the Precambrian ocean were much higher and controlled by chemical processes, specifically inorganic reactions such as the sorption of dissolved silica by various clays and precipitation of authigenic mineral phases such as opal-CT (Siever 1992). The newly evolved sponges and radiolarians in the Cambrian modified the Si biogeochemical cycle and began to utilize large quantities of dissolved silica. On the land angiosperms evolved, and with them a variety of plants that deposit biogenic silica, especially the grasses (Kaufman et al. 1983). However, it was the evolution of the diatoms beginning in the late Jurassic that drastically reduced dissolved silica concentrations and depressed concentrations to their present low level (Siever 1991).

Another explanation for the lighter silicification is physiological in that perhaps marine planktonic diatoms have become more proficient at constructing frustules. The formation of a frustule is an energy-requiring process (Werner 1977), and if heavy silicification is not necessary for survival it would seem that selective pressures would allow for diatoms to become more lightly silicified with time. If the oceans reached a new silica equilibria after the origin of radiolarians and diatoms or after a change in ocean circulation, then a stepwise reduction in silica content per cell would be expected, not a monotonic continuous decrease as exhibited by radiolarians (Moore 1969).

In short, we need to know the nature (direction, pattern, and amount) of change in diatom silica content and dissolved silica availability in the paleo-oceans before we can determine the controlling factors of diatom silica content. We conclude that marine planktonic diatoms probably have reduced their silica content downward and have evolved to species that are better adapted to ambient environmental conditions. By contrast, benthic diatoms are able to remain heavily silicified without losing a competitive advantage to more lightly silicified diatoms.

Acknowledgements

This paper is Contribution 2248 of UMCEES and R01911 of IFAS, University of Florida. PZ was partially supported by the South Florida Water Management District and the Carl S. Swisher Endowment Fund, and ET was partially supported by NSF grant BSR 88-18238.

Literature Cited

BARRON, J. A. AND J. G. BALDAUF. 1989. Tertiary cooling steps and paleoproductivity as reflected by diatoms and biosiliceous sediments. Pp. 341–354 *in* Productivity of the Ocean: Present and Past, W. H. Berger, V. S. Smetacek, and G. Wefer (Eds.), J. Wiley & Sons, Limited.

CONLEY, D. J., S. S. KILHAM, AND E. THERIOT. 1989. Differences in silica content between marine and freshwater diatoms. Limnol. Oceanogr. 34:205–213.

CZARNECKI, D. B. 1987. The freshwater diatom culture collection at Loras College, Dubuque, Iowa. The Acad. Nat. Sci. Phil. 465:1–16.

KAUFMAN, P.B., P. DAYANANDAN, Y. TAKEOKA, W. C. BIGELOW, J. D. JONES, AND R. ILER. 1983. Silica in shoots of higher plants, Pp. 409-449 *in* Silicon and Siliceous Structures in Biological Systems, T.L. Simpson and B.E. Volcani (Eds.), Springer-Verlag.

KRAUSSE, G. L, C. L. SCHELSKE, AND C. O. DAVIS. 1983. Comparison of three wet-alkaline methods of digestion of biogenic silica in water. Freshwater Biol. 13:1–9.

MCMILLAN, M., AND J. R. JOHANSEN. 1988. Changes in valve morphology of *Thalassiosira decipiens* (Bacillariophyceae) cultured in media of four different salinities. Br. phycol. J. 23:307–316.

MOORE, T. C., Jr. 1969. Radiolaria: Change in skeletal weight and resistance to solution. Geol. Soc. Amer. Bull. 80:2103–2108.

OLSEN, S. AND E. PAASCHE. 1986. Variable kinetics of silicon-limited growth in *Thalassiosira pseudonana* (Bacillariophyceae) in response to changed chemical composition of the growth medium. Br. phycol. J. 21:183–190.

PAASCHE, E. 1980a. Silicon content of five marine plankton diatom species measured with a rapid filter method. Limnol. Oceanogr. 25:474–480.

———. 1980b. Silicon. Pp. 259–284 *in* The Physiological Ecology of Phytoplankton, I. Morris (Ed.), Blackwell Scientific Press.

SIEVER, R. 1991. Silica in the oceans: biological-geochemical interplay, Pp. 287-295 *in* Scientists on Gaia, S. Schneider and P.J. Boston (Eds.), MIT Press.

———. 1992. Silica in the Precambrian. Geochim. Cosmochim. Acta 56:3265-3272.

STEIN, J. R. 1973. Handbook of Phycological Methods. Pp. 7–24, Cambridge University Press.

TAYLOR, N. J. 1985. Silica incorporation in the diatom *Coscinodiscus granii* as affected by light intensity. Br. phycol. J. 20:365–374.

VENRICK, E. L. 1978. How many cells to count? Pp. 167–189 *in* Phytoplankton Manual, A. Sournia (Ed.), UNESCO, Page Brothers Press.

WERNER, D. 1977. Silicate metabolism. Pp. 110–149 *in* The Biology of Diatoms, D. Werner (Ed.), University of California Press.

WILDERMAN, C. C. 1984. Techniques and results of an investigation into the autecology of some major species of diatoms from the Severn River estuary, Chesapeake Bay, Maryland, U. S. A. Pp. 631–643 *in* Proceedings of the 8th Diatom-Symposium, 1984, M. Ricard (Ed.).

The Morphology of Marine Genera of the Family Thalassiosiraceae Lebour Emend Hasle

by

I. V. Makarova

Komarov Botanical Institute of the Russian Academy of Sciences,
2 Popov Street, 197022 St. Petersburg P-22, Russia

with 4 plates

Abstract: Analysis of the morphological characters of the marine genera in the family Thalassiosiraceae has been undertaken. In light of the features that circumscribe these genera, two recently described species of the genus *Thalassiosira* Cleve must be accommodated into two new genera: *Takanao*, gen. nov and *Roundia*, gen. nov.

Introduction

Genera in the diatom family Thalassiosiraceae Lebour emend Hasle have distinctive features of strutted processes, number, and structure of pleurae and cribra, as well as shape and size of frustules and colony formation. The genus *Thalassiosira* Cleve is the largest of the family (which includes more than 130 species), and it is characterized by a high degree of variability relative to structure and placement of the morphological elements mentioned above. The family's other marine genera include but a few species (no more than five species in any one genus) and have marked defining features.

Labiate processes are found in all centric diatoms; their characteristic features of construction help to define taxa. This is especially well-demonstrated in the families Pyxidiculaceae Nikolaev, Coscinodiscaceae Kützing, Hemidiscaceae Hendey emend Simonsen and, in the latter, processes are the same as in the genus *Actinocyclus* and others. The other processes in the class Centrophyceae are characterized not only by their form and size, but by their number and disposition on the valve. Usually they are numerous and occupy definite positions; three types of positioning have been distinguished (The Diatoms of the USSR, 1988:18). Rarely they are in pairs or singular.

As a rule there is a single labiate process in members of family Thalassiosiraceae with the exception of some species of the genus *Thalassiosira* (*T. symmetrica* G. Fryx. et Hasle, *T. elsayedii* G. Fryx., *T. hendey* Hasle et G. Fryx., *T. simonsenii* Hasle et G. Fryx., *T. punctifera* (Castr.) Hasle and *Planktoniella sol* (Wallich) Schütt, which have two processes, and others which have (rarely) more (e.g., *T. baltica* (Grun.) Ostf., *T. tumida* (Janisch) Hasle). Usually the labiate process is situated in the ring of marginal strutted processes.

Exceptions are found in the genus *Minidiscus* Hasle, where the labiate process is found in the center of the valve and in *Sceletonema* Greville, where labiate processes are found in the terminal cells.

This paper describes and compares distinctive features of the marine genera of the Thalassiosiraceae. In light of these features, the taxonomic position of two species described as members of the genus *Thalassiosira* are considered.

Materials and Methods

The collection of the author, samples kindly provided by colleagues, and data from the published literature served as the basis for detailed study and analysis of morphologic characteristics of the genera in the family Thalassiosiraceae. Photomicrographs were obtained with a JEOL JSM-35C scanning electron microscope (SEM).

Terminology for morphological features follows Anonymous (1975) and Ross et al. (1979).

Results and Discussion

The labiate process in the genus *Thalassiosira* may occur in one of three positions. In most species it is situated in the marginal ring of strutted processes, but it may occur inside of the valve margin (*T. confusa* Makar., *T. latimarginata* Makar., *T. poroseriata* [Ramsfjell] Hasle and others), or near the center of the valve (*T. oestrupii* [Ostf.] Hasle, *T. bioculata* [Grun.] Ostf., *T. poro-irregulata* Hasle et Heimdal, *T. ritscheri* [Hust.] Hasle, *T. proschkinae* Makar., *T. pseudomultipora* Makar., and some others).

The form and size of labiate processes are characteristic features for each genus in the Thalassiosiraceae. In *Thalassiosira*, the labiate process on the internal surface is presented, as a rule, by a flattened infundibulum or short tube with a slit, which is often orientated radially or, rarely, tangentionally. On the external surface the labiate process is represented by a noticeable tube, which terminates as a round hole (Figs. 1–9). In *Sceletonema*, a short portion of the labiate process is situated on the internal surface (Fig. 16), and a short or a long tube is found on the external surface. In *Bacterosira* Gran and *Planktoniella*, the labiate process is represented by a relatively small tube on the external surface (in each genus it has different form) and a slit that is rounded by the two lips on the internal surface (Figs. 11, 14). In the genus *Porosira* Jørg., the labiate process differs by having a very large expression internally, and externally it is represented by a hole or low tube (Figs. 15, 18–20). In both *Lauderia* Cleve and *Detonula* Schütt, the labiate process has a large external tube (Fig. 10) and is large on the internal surface. As for the genus *Minidiscus*, it has a very small labiate process or a rather noticeable tube on the external surface. *Coenobiodiscus* Loeblich, Wight and Darley has its labiate process represented by an elongated or round hole externally, and inside it has a considerable part in the form of the tube which is flattened and extended at the end (Figs. 12, 13, 17).

As for the characteristic features for this family (and the order Thalassiosirales Gleser et Makar. as well), the structure and position of the strutted processes should be noted for each genus. In the species of the genus *Thalassiosira*, the strutted processes may form a single (rarely two) marginal ring, or be scattered on the valve face (Makarova, 1988, Pl. XIII, Figs. 1–13; Pl. XIV, Figs I,II). As for the shape and size of the strutted processes, they can possess a long tube on the external or internal valve surfaces. In the latter case, they are represented on the exterior by a round hole only (Figs. 21–26) or they have short tubes or lack internal tubes (Figs. 27–29). There is a single strutted process in the center or, if there are several, then they can form a straight or curved line, a ring or cluster (Figs. 30–33). The number of the satellite pores may be 3–4, rarely 5 (Figs. 29–31). In

the genus *Lauderia*, the marginal strutted processes have a tube of considerable length on the exterior surface and a small tube on the interior. They are situated on the valve margin and valve mantle as on a chessboard. The long, occluded processes are situated behind the strutted processes on the border with the valve face. Sometimes strutted processes are situated in the center or on the valve face (Fig. 34). In the genus *Sceletonema*, strutted processes are tube-like or fissure-chute in form with three supports, and they form a marginal ring (Fig. 35). In the genus *Detonula*, marginal strutted processes on the exterior of the valve have an original shape of a long tube sloping at the end or the second semitube (Fig. 36). Internally they have a tube with four satellite pores. There are one–two processes in the center of the valve; they have three–four satellite pores. In *Porosira*, strutted processes on the inside of the valve have a slightly projected tube, surrounded by two–four satellite pores. They terminate on the outer surface by a hole, the diameter of which is larger than a foramen (Figs. 15, 37), or by a narrow tubule. These processes form the marginal ring and are scattered on the valve face. In the genus *Bacterosira*, strutted processes form a single marginal ring and are clustered in the center. Their small tube is projected above the external surface of the valve and internally the small tube is surrounded by three–four satellite pores (Figs. 38–41).

The number and the structure of the pleurae also helps to define each genus. For example, they are numerous and complex in the genera *Lauderia* and *Detonula*, less numerous in the genus *Porosira*, and few in the genus *Thalassiosira*. The unique structural and positional aspects of these features, as well as the combinations of characters, serve to define the genera of this family.

Analysis of representatives of the Thalassiosiraceae shows that two newly described species of *Thalassiosira*, *T. bingensis* Takano (1980) and *T. cardiophora* Round (1988), are morphologically very different from the other species of the genus and from the other genera. Taking into consideration such characters of *T. bingensis* as shape of the large strutted processes, which form a marginal ring, the occurrence of the second ring on the mantle consisting of small strutted processes, position of two labiate processes surrounded by small arcs formed by strutted processes, and an unusual cingulum, it is reasonable to consider it as a new genus of the family. The name *Takanoa* gen. nov. is proposed to honor H. Takano.

The second species, *T. cardiophora*, is distinguished by many characters. These include a large number of areolate pleurae, unusual shape of marginal strutted processes with five flanges forming a curved arc near the labiate process, and the quite small, oval hole of the labiate process on the external surface of the valve. All of these distinctive features make it possible to separate this species into a new genus, *Roundia*, gen. nov., named in honor of F. E. Round.

Descriptions of these newly proposed genera follow:

Takanoa Makar. gen. nov.
Cellulae solitariae magnae. Frustula cylindrica valvacopula collariformi areolata et pleuris anulatis ligulatis praedita. Valvae planae. Areolae tenuissimae, radialiter seriatae, seriebus fasciculatis. Foramen externum, cribrum internum. Fultoportulae peculiares magnae marginales, inter quas rimoportulae duae quoad diametrum subopppositae tubo externo longo praeditae, fultoportulis aliquot parvis arcum formatis circumcinetae. Fultoportula centralis una et praeterea aliquot per valvam dispersae. Limbus sat altus, tenuiter areolatus, fultoportulis marginalibus haud crebris anulatim praeditus.

Species typica: *Takanoa bingensis* (Takano) Makar. comb. nov. Basionym: *Thalassiosira bingensis* Takano (1980:42).

Roundia Makar. gen. nov.
Cellulae solitariae. Frustula alte cylindrica, valvocopula areolata latiore et pleuris pluribus areolatis ligulatis praedita. Valvae planae, spines et granulis parvis minutae, areolis indistincte dispositis. Areolae foramine externo minimo donatae. Fultoportulae marginales eminentiis 5 praeditae, nonnullae prore rimoportulam arcum formantes, se invicem approximatae. Rimoportula una ore ovali minimo ad faciem valvae externam praedita. Limbus humillimus.

Species typica: *Roundia cardiophora (Round) Makar. comb. nov. Basionym: Thalassiosira cardiophora* Round (1988:126).

Detailed description of these species is provided in the works of Takano (1980) and Round (1988).

Acknowledgements

The author is grateful to the colleagues who gave their collections and engineers L. A. Karzeva and N. V. Chenzova, who provided the work of SEM. Thanks are due to F. E. Round and R. Ross for discussions about my poster during the Symposium.

Literature Cited

ANONYMOUS. 1975. Proposal for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53:323–354.

THE DIATOMS OF THE USSR. 1988. Vol. II, fasc. I. 115 p.

MAKAROVA, I. V. 1988. The diatoms of the seas USSR: Genus *Thalassiosira* Cl. "Nauka." Leningard. 115 p.

ROSS, R., E. J. COX, N. I. KARAJEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

ROUND, F. E. 1988. A new species of *Thalassiosira*, *T. cardiophora*. Diatom Res. 3:123–127.

TAKANO, H. 1980. New and rare diatoms from Japanese marine waters. IV. *Thalassiosira bingensis* sp. nov. Bull. Tokai. Reg. Res. Lab. 103:41–53.

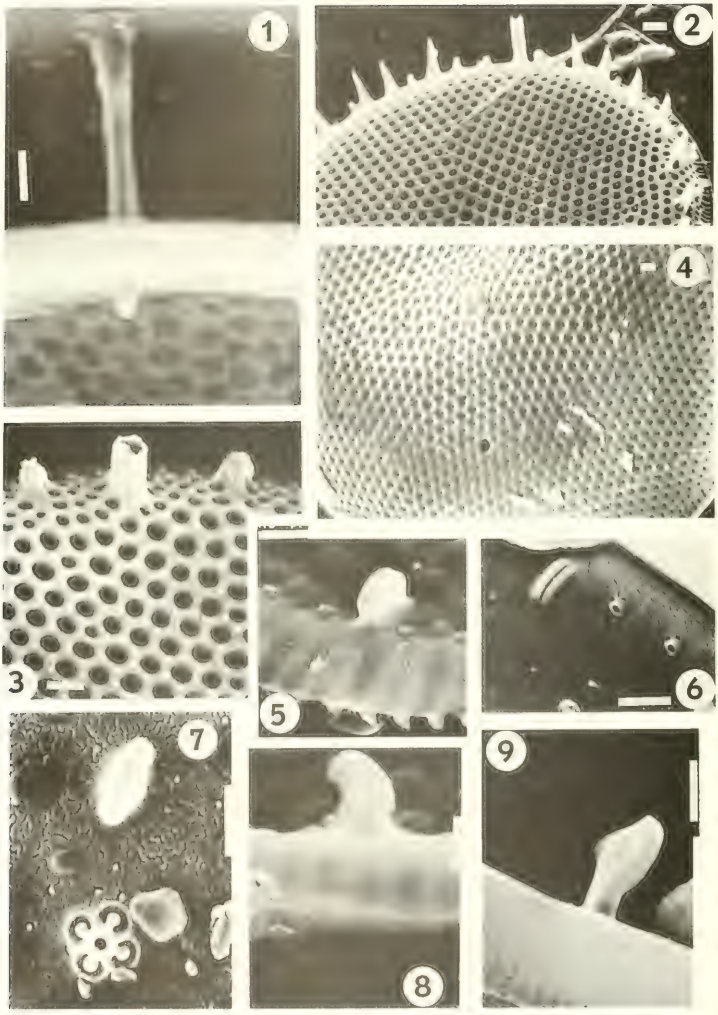
Explanation of Plates

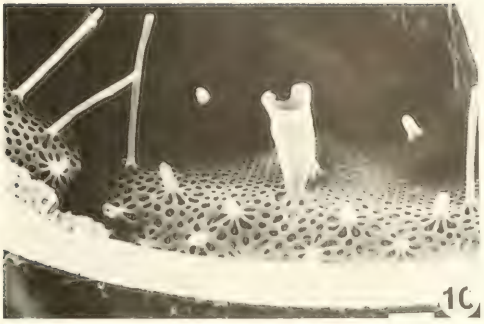
Plate 1, Figures 1–9
FIGURES 1–9. Shape and location of labiate process in *Thalassiosira* Cleve. FIGURES 1–4. Labiate process, external views. FIGURE 1. Narrow and long external tube and short internal tube (*T. nordenskioeldii* Cleve). FIGURES. 2, 3. Cylindrical tube. FIGURE 2. Labiate process among spines (*T. eccentrica* (Ehrenberg) Cleve). FIGURE 3. Labiate process in the marginal ring of strutted processes (*T. anguste-lineata* (W. Sm.) G. Fryx.) FIGURE 4. Labiate process in middle of radius, without external tube (*T. plicata* Schrader). FIGURES 5–9. Labiate process, internal views. FIGURE 5. Flattened, short tube (*T. antarctica* Comber). FIGURE 6. Slit with two lips (*T. hyalina* (Grun.) Gran). FIGURE 7. Labiate process near center of valve, with flattened funnel (*T. pseudomultipora* Makar.). FIGURES 8, 9. Labiate process with large specific internal part. FIGURE 8. *T. bramaputrae* var. *septentrionalis* (Grun.) Makar. FIGURE 9. *T. tumida* (Janisch) Hasle. Scale bars = 1 μm.

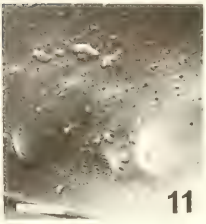
Plate 2, Figures 10–20
FIGURES 10–20. Shape and location of labiate processes in different genera of the family Thalassiosiraceae. FIGURES 10–13. Labiate processes, external views. FIGURE 10. Large tube with wide hole (*Lauderia annulata* Cleve). FIGURE 11. Short tube with narrow hole (*Bacterosira concavo-convexa* Makar.). FIGURES 12, 13, 15. External tube lacking. FIGURES 12, 13. *Coenobiodiscus muriformis* Loeblich, Wight and Darley. FIGURE 15. *Porosira glacialis* (Grun.) Jørg. FIGURES 14, 16–20. Labiate process internal views. FIGURE 14. Slit surrounded by two lips (*Bacterosira concavo-convexa* Makar.). FIGURE 16. Short flattened tube (*Sceletonema costatum* (Grev.) Cleve). FIGURE 17. Short, wide, and flattened tube (*Coenobiodiscus muriformis* Loeblich, Wight and Darley). FIGURES 18–20. Large part with long slit. FIGURES 18, 19. *Porosira glacialis* (Grun.) Jørg. FIGURE 20. *P. punctata* (Jousé) Makar. Scale bars = 1 µm.

Plate 3, Figures 21–33
FIGURES 21–33. Shape, size of marginal strutted processes and location, number of central strutted processes in the genus *Thalassiosira*. FIGURES 21–24, 33. Strutted processes, external views. FIGURE 21. Long external tubes (*T. nidulus* (Brun) Jousé). FIGURE 22. Very short tubes (*T. mala* Takano). FIGURE 23. External tubes lacking (arrows) (*T. oestrupii* var. *venrickae* G. Fryx. et Hasle). FIGURE 24. Bulboformis tubes (*T. bulbosa* Syvertsen). FIGURES 25–32. Strutted processes, internal views. FIGURES 25,26. Long tubes with 4 satellite pores (*T. pseudomultipora* Makar.). FIGURE 27. Short tube with 3 satellite pores (*T. tumida* (Janisch) Hasle). FIGURE 28. Very short tubes with 4 satellite pores (*T. bramaputrae* (Ehrenberg) Hakannson et Locker). FIGURE 29. Internal tubes lacking (*T. antaractica* Comber). FIGURE 30. One range (*T. confusa* Makar.). FIGURE 31. Central ring (*T. tumida* (Janisch) Hasle). FIGURE 32. Cluster (*T. hyalina* (Grun.) Gran). FIGURE 33. One central process (*T. aestivalis* Gran). Scale bars = 1 µm.

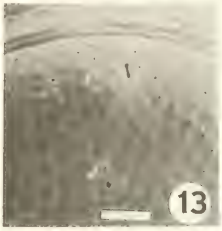
Plate 4, Figures 34–41
FIGURES 34–41. Shape and location of strutted processes in different genera of the family Thalassiosiraceae. FIGURES 34–39. Strutted processes, external views. FIGURES 34–36. Marginal ring with long tubes of different shape. FIGURE 34. *Lauderia annulata* Cleve. FIGURE 35. *Sceletonema costatum* (Grev.) Cleve. FIGURE 36. *Detonula pumila* (Castr.) Schütt. FIGURE 37. Large hole on external surface of valve (arrows) (*Porosira punctata* [Jousé] Makar.). FIGURE 38. External tube lacking (arrows) (*Bacterosira fragilis* Gran, resting spore). FIGURE 39. Short tubes (*Bacterosira concavo-convexa* Makar.). FIGURES 40, 41. Strutted processes, internal views. FIGURE 40. Central processes with 3–4 satellite pores (*Bacterosira concavo-convexa* Makar.). FIGURE 41. Marginal processes with 4 satellite pores (*Coenobiodiscus muriformis* Loeblich, Wight, and Darley). Scale bars = 10 µm in FIGURE 34 and 1 µm in FIGURES 35–41.


1
2
4
3
5
6
7
8
9

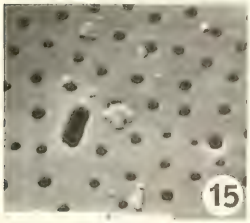

10

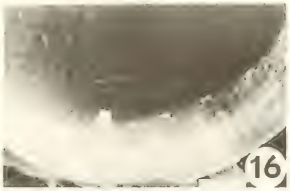

11

12

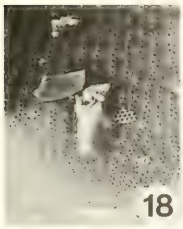

13

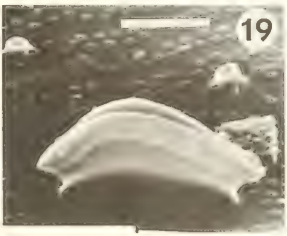
14

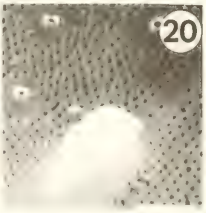

15

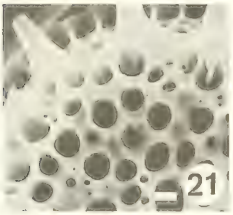

16

17

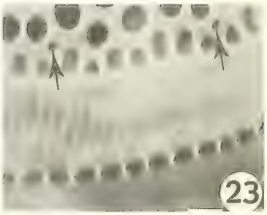

18


19


20


21

22


23

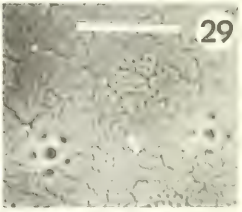
24

25

26

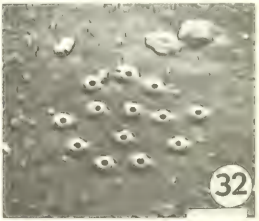
27

28

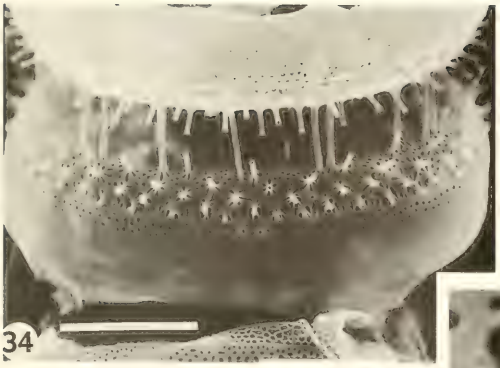

29

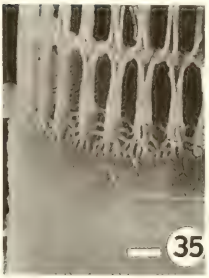
30

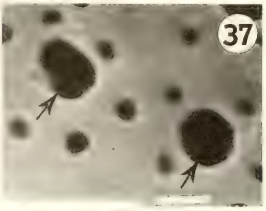
31

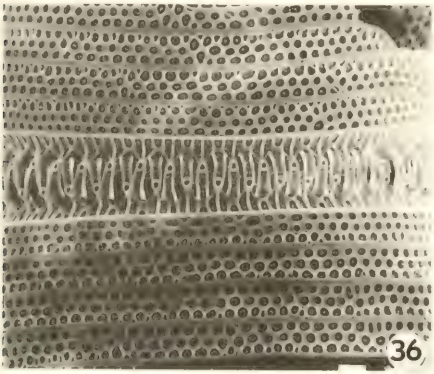

32

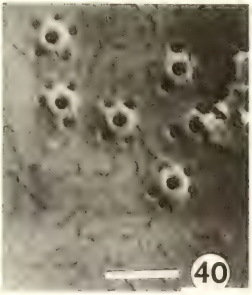
33

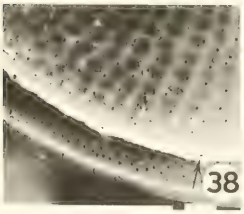

34


35

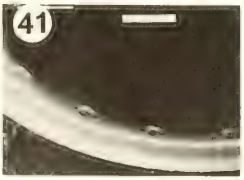

37


36


40


38

39


41

Morphology of Three Related *Coscinodiscus* Ehrenberg Taxa From the Southern Gulf of Mexico and Coastal North Pacific of Mexico

by

Luis Moreno

Instituto de Ciencias del Mar y Limnologia,
Universidad Nacional Autónoma de México, Apartado Postal 70-305,
Mexico 04510 D. F.

and

Sergio Licea

Instituto de Ciencias del Mar y Limnologia,
Universidad Nacional Autónoma de México, Apartado Postal 70-305,
Mexico 04510 D. F.

with 4 plates and 2 tables

Abstract: Light and electron microscopic observations were made on fossil and Recent marine material of *Coscinodiscus perforatus* var. *cellulosa* Grunow, *C. perforatus* var. *pavillardi* (Forti) Hustedt, and *C. radiatus* Ehrenberg. Morphological variation of macrorimoportulae, rimoportulae, areolar array, and angle of separation between macrorimoportulae suggested that these three taxa are very similar. We propose that *C. perforatus* var. *cellulosa* and *C. perfortus* var. *pavillardi* belong to *C. radiatus*. Sancetta (1987) suggested that *C. perforatus* and *C. radiatus* are conspecific, and our study, based on additional characteristics, supports her conclusion.

Introduction

Description of the genus *Coscinodiscus*, as well as a considerable number of species within the genus, were made originally from fossil material by Ehrenberg between 1838 and 1854 (*vide* Sancetta 1987). The generic diagnosis mentioned by Ehrenberg in 1839 (*vide* Hasle and Sims 1986) was very brief. It indicated size of the areolae and their array on the valve as the only characters, and no generitype was designated. Problems referring to the typification of the genus have been dealt with in different ways by Boyer (1927),

Jousé (1963), Ross and Sims (1974), and Fryxell (1978). Brooks (1975) and Sims (1989) have emphasized that it will be necessary to analyze the species of this genus in more detail and to define the limits of each. At present, several features are considered distinctive of the genus, including presence of external vela, a marginal ring of rimoportulae, and the absence of fultoportulae, spines, and a pseudonodulus (Halse and Sims 1986; Fryxell and Ashworth 1988).

Since the advent of the scanning electron microscope (SEM), many *Coscinodiscus* species have been reassigned to other genera, such as *Thalassiosira* (Hasle and Fryxell 1977; Akiba and Yanagisawa 1986), *Psammodiscus* (Round and Mann 1980), *Thalassiosiropsis* (Hasle and Syvertsen 1985), *Azpeitia* (Fryxell et al. 1986) and *Stellarima* (Hasle et al. 1988). The result of this activity has been a noticeable reduction in the number of recognized *Coscinodiscus* species. In this regard, Sancetta (1987) has suggested that *C. perforatus* may be a form of *C. radiatus*.

The objective of this paper is to compare the valve morphology of *C. perforatus* var. *cellulosa* Grunow, *C. perforatus* var. *pavillardi* (Forti) Hustedt, and *C. radiatus* Ehrenberg through examination of Recent as well as late Miocene material from different parts of Mexico, and to evaluate their taxonomic identities.

Materials and Methods

Recent material was collected between March 1971 to September 1989 from the Bahia de Campeche, an area to the south of the Gulf of Mexico, between 18°15' to 23°39.1' N latitude and 91°02' to 97°19.7' W longitude.

Fossil material was obtained from the following stratigraphic sections:

(1) Valle de Diatomita, in Bahía Asuncíon, southern Baja California, 27°11'29' N latitude, 114°20'55'' W longitude. It is of late Miocene age.

(2) San Felipe I and II, from Baja California, 31°06'29'' N latitude, 114°56'25'' W longitude, from the San Felipe section. This material is of late Miocene age.

(3) Arroyo Hondo, María Madre Island, Nayarit, 21°39'11'' N latitude, 106°35'05'' W longitude. It is of late Miocene-early Pliocene age.

Permanent preparations for light microscopy (LM) and SEM were obtained following a technique suggested by Moreno (1990). This technique is based on the cleaning methods of Hasle and Fryxell (1970), Simonsen (1974), and Schrader (1976). Terminology follows that suggested by Ross and Sims (1972), Anonymous (1975), Brooks (1975), and Ross et al. (1979).

Results

Each taxon is illustrated and described briefly, and references used in the identification of the taxon are listed. LM and SEM observations and descriptions are then presented.

Coscinodiscus perforatus var. **cellulosa** Grunow
(Figs. 1, 5–11, Table 1)

REFERENCES: Rattray 1889, p. 572; Hustedt 1930, p. 447, Fig. 246; Cupp 1943, p. 61, Figs. 25Aa–f; Cleve-Euler 1951, p. 66, Fig. 100c; Van der Werff and Huls 1957–1974, C.AIc.15.

TABLE 1. Valve morphometrics of *Coscinodiscus* spp., including some observations from literature.

Coscinodiscus	Author	Locality	Number of valves	Diameter in µm	Central areolae in 10 µm	Marginal areolae in 10 µm	Marginal striae in 10 µm	Areolae of central rosette	Areolae surrounding central areola
C. perforatus var. *cellulosa* Grun.	This study	South Gulf of Mexico	13	48.9 - 108.0	5 - 8	5 - 9	8 - 18	6 - 11	—
		Valle Diatomita	1	127.5	4 - 5	4 - 5	7 - 8	12	—
		San Felipe	2	116.3 - 120.0	4 - 5	4 - 6	7 - 9	7 - 8	—
		Arroyo Hondo	6	101.4 - 182.5	3 - 5	3 - 5	7 - 11	8 - 14	—
	Rattray 1889			135 - 150	3 - 5	—	—	—	—
	Hustedt 1930			90 - 200	3.5 - 5.5	—	8	13	—
	Cupp 1943			90 - 110	4.5	4.5 - 5	8	5	—
	Cleve-Euler 1951			100 - 150	2.5 - 4	—	—	8	—
	Van der Werff & Huls 1957 1974			90 - 200	4 - 5	6 - 8	—	6	—
C. perforatus var. *pavillardi* (Forti) Hust.	This study	South Gulf of Mexico	32	23.8 - 132.5	3 - 8	4 - 8	6 - 19	4 - 7	5 - 7
		Valle Diatomita	1	29.5	7	7	14	5	—
		Arroyo Hondo	2	40.6 - 50.0	5	5	15 - 18	5	—
	Hustedt 1930			90 - 200	3.5 - 5.5	—	—	5 - 13	—
	Cupp 1943			143 - 270	4.5	4 - 5	—	5 - 7	—
	Van der Werff & Huls 1957 1974			90 - 200	±4	±6	—	7	—
C. radiatus Ehr.	This study	South Gulf of Mexico	39	20.0 - 97.5	4 - 10	4 - 10	7 - 22	4 - 8	6 - 7
		Valle Diatomita	4	33.0 - 81.3	5 - 8	5 - 8	9 - 14	5 - 7	—
		Arroyo Hondo	4	25.6 - 135.0	4 - 7	4 - 7	—	5 - 6	—
	Rattray 1889			67.5 - 180	2 - 2.5	6	—	—	—
	Hustedt 1930			30 - 180	2 - 4	4 - 9	6 - 8	5	—
	Cupp 1943			35 - 60	3 - 4	6 - 7	9 - 11	6	—
	Cleve-Euler 1951			60 - 125	2 - 2.5	5 - 6	—	—	7
	Van der Werff & Huls 1957 1974			30 - 180	2 - 4	4 - 9	8	5 - 14	—
	Hasle & Sims 1986			40 - 90	4 - 6	6 - 8	—	6 - 8	6
	Sancetta 1987			13 - 100	3.5 - 5	6 - 8	—	5 - 6	7
	Fryxell & Ashworth 1988			28 - 118	4.2 - 5.2	4 - 5	—	6 - 8	—

— = No data available

DESCRIPTION: Valves circular, convex, flat, or concave, 48.9–182.5 µm in diameter. Two asymmetrical macrorimoportulae separated at 135–146° to one another. Central areolae 3–8 in 10 µm, marginal areolae 3–9 in 10 µm, rimoportulae 2–4 in 10 µm, striae 7–18 in 10 µm and 6–14 areolae in inconspicuous rosette (Tables 1, 2). A distinctive feature for this taxon is a defined central area with variable number of areolae around its periphery (Figs. 1, 5, 9, 10).

In the light microscope rimoportulae and macrorimoportulae are difficult to observe. Primary and secondary radial rows of areolae are observed; the areolae are hexagonal to pentagonal, sometimes having a spherical appearance (Fig. 1).

SEM observations of the interior show eccentric rimoportulae (Figs. 5, 6) and a marginal ring of rimoportulae (Fig. 5) separated from the margin by 0.5–1 areola (Fig. 8). Two asymmetrical macrorimoportulae (Fig. 5) are tubular in form and wide at the base and bulbous at the apex, with a circular (Fig. 7) or elliptical (Fig. 11) external aperture. Near the valve margin circular foramen are observed and siliceous struts project and join the mantle to form a "circular siliceous bridge" (Figs. 7, 8).

The exterior of this diatom viewed with SEM shows the central area surrounded by areolae (Figs. 9, 10). A pore or notch is situated near the periphery of the central area (Fig. 10). In the immediate eccentric zone, small pores that may be the exterior openings of the rimoportulae are found (Fig. 10). A notch in the mantle is conspicuous and corresponds to the exterior aperture of a macrorimoportulae (Fig. 9, see also Fig. 7). Siliceous struts or filaments from the base of the membrane of the reticular cribra can be observed at the submarginal level (Fig. 11).

Coscinodiscus perforatus var. **pavillardi** (Forti) Hustedt
(Figs. 2, 3, 12–21, Tables 1, 2)

REFERENCES: Hustedt 1930, p. 447, Figs. 247a–e; Cupp 1943, p. 62, Figs. 25Ba–e; Van der Werff and Huls 1957–1974, C.AIc.15

DESCRIPTION: Valve circular, concave to concave-convex, 23.8– 132.5 µm in diameter. Two asymmetrical macrorimoportulae separated 131–145° from one another, central areolae 3–8 in 10 µm, marginal areolae 4–8 in 10 µm, rimoportulae 2–4 in 10 µm, marginal striae 6–19 in 10 µm, and 4–7 areolae forming a distinct central rosette. A central areola can sometimes be surrounded by 5–7 areolae (Tables 1, 2).

There appears to be a central rosette formed by a variable number of areolae, and from this rosette the primary radial rows originate. Secondary radial rows can be seen outside this zone (Figs. 12, 13), along with the eccentric rimoportulae (Figs. 12, 14).

In the light microscope the macrorimoportulae can be seen as notches (Figs. 2, 3). The rimoportulae can be observed with some difficulty with brightfield optics, and with this technique they appear as small marginal swellings turned to the valve center (Fig. 2).

SEM observations on the interior show a ring of rimoportulae both in the mantle and near the center of the valve (Fig. 12). Marginal rimoportulae are separated from the mantle by 0.5–1 areola (Fig. 15). The asymmetrical macrorimoportulae are tubes that are wide at the base, bulbous at the apex, and curved on the lower side towards the apex (Figs. 16, 17). The suture filaments of the exterior cribra can also be observed. Marks of these filaments look like short striae, and the walls of the areolar chambers look like thick striae (Figs. 15–17). The exterior of the macrorimoportulae is circular in shape (Fig. 16). Macrorimoportulae (Fig. 16) have a tubular structure that widens at the base (Fig. 17). The central rosette can be seen through the exterior cribra between the interior aperture

of five areolae in the eccentric foramina and the marks of the areolar chambers. These chambers can be heptagonal, hexagonal, or pentagonal (Fig. 13).

Externally, the concavity of the valve is characteristic of this variety (Fig. 18). The exterior aperture of eccentric rimoportulae and macrorimoportulae are evident (Figs. 18, 19). There are two elements of the cingulum, a wider one corresponding to the valvocopula and a thinner one, which is the copula (Fig. 19). In a typical frustule, there are three bands: a thin pleura with ligula; the copula, which is also thin; and the valvocopula, which is a wider band. Likewise, the three bands show fine transverse pores (Figs. 20, 21). The reticular membrane of the cribra can be observed in the marginal areolae as well as the mantle (Fig. 19).

Coscinodiscus radiatus Ehrenberg
(Figs. 4, 22–40, Tables 1, 2)

REFERENCES: Rattray 1889, p. 514; Hustedt 1930, p. 420, Figs. 225a, b; Cupp 1943, p. 56, Figs. 20a–d; Cleve-Euler 1951, p. 65, Figs. 97a, b; Van der Werff and Huls 1957–1974, C.AIc.15; Hasle and Sims 1986, p. 310, Figs 8–32; Sancetta 1987, p. 234, Figs. 1–10; Fryxell and Ashworth 1988, p. 363, Figs. 3, 9, 10, 15, 19, 27.

DESCRIPTION: Valves circular, convex, concave or flat, 20.0–135.0 µm in diameter, central and marginal areolae 4–10 in 10 µm, rimoportulae 2–4 in 10 µm. Two macrorimoportulae, separated at 132–147°. Striae 7–22 in 10 µm, and there is a central rosette of 4–8 areolae. Sometimes there may be a central areola surrounded by 6–7 areolae (Tables 1, 2; Fig. 31). A central rosette may be formed by a variable number of areolae and eccentric rimoportulae (Figs. 22, 28, 29, 31).

In the light microscope two small asymmetrical notches representing the macrorimoportulae are evident at the edge of the mantle (Fig. 4). On the margin of the valve there are striae that correspond to the walls of the locular chambers (Fig. 4).

SEM observations of the interior show a ring of rimoportulae, tubular towards the mantle and oriented towards the valve center (Figs. 22, 23), which are separated from the edge of the mantle by 0.5–1 areolae (Figs. 23, 24). Macrorimoportulae are tube-like, wide at the base, and bulbous at the apex (Fig. 24). Rimoportulae and macrorimoportulae sometimes seem to have broken pieces (Figs. 22, 23), but this may be caused by the valves being in an early phase of development. We can observe the base of the walls of the locular chambers resembling striae on the circular siliceous bridge (Fig. 23). The central rosette is also observed indirectly through the interior aperture of six loculi (Figs. 22, 28) and the locular chambers are also evident. Areolae can be heptagonal, hexagonal, or pentagonal (Figs. 39, 40), and they show the primary and secondary radial rows of areolae (Figs. 38, 40).

SEM observations of the exterior show the apertures of both eccentric and mantle rimoportulae are evident (Figs. 26, 27, 29, 31, 32, 34, 35), and the aperture of the macrorimoportulae can also be seen (Fig. 31). The center of the valve has a central rosette (Fig. 29) or a central areola surrounded by several areolae (Fig. 31). The girdle is formed by three bands. Girdle elements include a thin, ligulae pleura, a thin copula, and wide valvocopula. All elements are perforated (Figs. 32–37).

Discussion

Data obtained from a survey of the literature and the present study suggest the greatest variation in morphological features of the taxa considered is in the number of central and

TABLE 2. Rimoportulae and macrorimoportulae morphometrics of *Coscinodiscus* spp., including some observations from literature.

Coscinodiscus	Author	Locality	Rimoportulae in 10 µm	Number of macrorimoportulae	Angle of separation macrorimoportulae
C. perforatus var. *cellulosa* Grun.	This study	South Gulf of Mexico	2 - 4	2	139° - 146°
		Arroyo Hondo	2 - 3	2	135° - 142°
	Rattray 1889		2	–	–
C. perforatus var. *pavillardi* (Fort.) Hust.	This study	South Gulf of Mexico	2 - 4	2	131° - 145°
		Valle Diatomita	–	2	139°
		Arroyo Hondo	2 - 3	2	136°
	Cupp 1943		–	2	–
C. radiatus Ehr.	This study	South Gulf of Mexico	2 - 4	2	132° - 147°
		Valle Diatomita	–	2	137°
		Arroyo Hondo	3	2	–
	Hasle & Sims 1986		3 - 4	2	135°
	Sancetta 1987		3	2	–
	Fryxell & Ashworth 1988		1 - 2	2	120° - 135°

– = No data available

terminal areolae, as well as number of rimoportulae (Tables 1, 2). This variation is not unexpected, however, since these characters are difficult to observe under the light microscope. For the feature of angle of separation of the macrorimoportulae, reported by Hasle and Sims (1986) and Fryxell and Ashworth (1988) for *Coscinodiscus radiatus* only, values were greater in specimens observed in the present study than reported previously (Table 2).

It is interesting to note that there are morphological similarities between *C. perforatus* var. *cellulosa*, *C. perforatus* var. *pavillardi*, and *C. radiatus*, as Moreno (1990) had observed previously. Similarities exist particularly with regard to the form of rimoportulae and macrorimoportulae, cribra, mantle, and in the presence of primary and secondary radial rows of areolae (Figs. 9, 12, 22, 39–40). In this regard Fryxell and Ashworth (1988) point out that the primary radial rows start in the central area from a hexagonal areola and the secondary radial rows appear in the middle part of the valve starting from a pentagonal areola. In the present study, however, primary radial rows were observed to originate from a heptagonal, hexagonal, or pentagonal areola. Secondary radial rows can begin at any level, either near the central area or near the margin, and the areolae can be hexagonal or pentagonal. Also, a central areolae appears surrounded by several areolae as shown in Cleve-Euler (1951, Fig. 97a), Halse and Sims (1986, Fig. 34) and Sancetta (1987, pl. 2, Fig. 6). The three-part girdle, composed of finely perforated bands, including two thin and one wide, is a feature that had previously been reported for *C. radiatus* only (Hasle and Sims 1986).

It is important to note that with respect to both qualitative (presence/absence) and quantitative (densities, etc.), features there was no difference between material from Recent collections and material from the late Miocene. This suggests conservation of phenotype through time in these forms.

Results of this study and our survey of the literature lead us to conclude that *C. perforatus* var. *cellulosa* and *C. perforatus* var. *pavillardi* correspond to *C. radiatus*. Sancetta (1987) suggested previously that *C. perforatus* and *C. radiatus* are conspecific. Our results support her conclusion, and therefore *C. perforatus* var. *cellulosa* Grunow and *C. perforatus* var. *pavillardii* (Forti) Hustedt are later synonyms of *C. radiatus* Ehrenberg.

Finally, we suggest the term "circular siliceous bridge" be used to designate the structure situated at the base of the valve that joins the elements of the cribra, walls of the locular chambers, and internal foramina.

Acknowledgements

We are indebted to Ana Luisa Carreño for placing at our disposal material from Valle de Diatomita and Arroyo Hondo, to Vicente Ferreira for his dedicated support in collecting material and for supplying some samples from the San Felipe section, to Margarita Reyes for assistance at the SEM of the Institute of Geology, National University of Mexico, and to Carina Lange for critical suggestions to this work.

Literature Cited

AKIBA, F. AND Y. YANAGISAWA. 1986. Taxonomy, morphology and phylogeny of the Neogene zonal marker species in the middle-to-high latitudes of the north Pacific. Init. Repts. Deep Sea Drilling Project 87:483–557.

ANONYMOUS. 1975. Proposals for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53:323–354.

BOYER, C. S. 1927. Synopsis of North American Diatomaceae. Part I. Coscinodiscatae, Rhizosolenatae, Biddulphiatae, Fragilariatae. Proc. Acad. Nat. Sci. Phila. 78:1–583.

BROOKS, M. 1975. Studies on the genus *Coscinodiscus*. I. Light, transmission and scanning electron microscopy of *C. concinnus* Wm. Smith. Bot. Mar. 18:1–13.

CLEVE-EULER, A. 1951. Die Diatomeen von Schweden und Finnland. Kungl. Svenska Vetenskapsakademiens Handl. 4:1–163.

CUPP, E. E. 1943. Marine plankton diatoms of the West Coast of North America. Bull. Scripps Inst. Oceanogr. 5:1–237.

FRYXELL, G. A. 1978. Proposal for the conservation of the diatom *Coscinodiscus argus* Ehrenberg as the type of the genus. Taxon 27:122–125.

FRYXELL, G. A. AND T. K. ASHWORTH. 1988. The diatom genus *Coscinodiscus* Ehrenberg: characters having taxonomic value. Bot. Mar. 31:359–374.

FRYXELL, G. A., P. A. SIMS, AND T. P. WATKINS. 1986. *Azpeitia* (Bacillariophyceae); related genera and promorphology. Syst. Bot. Monog. 13:1–74.

HASLE, G. R. AND G. A. FRYXELL. 1970. Diatoms: cleaning and mounting for light and electron microscopy. Trans. Am. Microsc. Soc. 89:469–474.

———. 1977. The genus *Thalassiosira*: some species with a linear areola array. Pp. 15–66 *in* Proceedings of the Fourth Symposium on Recent and Fossil Marine Diatoms, R. Simonsen, ed. O. Koeltz, Koenigstein.

HALSE, G. R. AND P. A. SIMS. 1986. The diatom genus *Coscinodiscus* Ehrenberg *C. argus* Ehrenberg and *C. radiatus* Ehrenberg Bot. Mar. 29:305–318.

HASLE, G. R. AND E. E. SYVERTSEN. 1985. *Thalassiosiropsis*, a new diatom genus from the fossil records. Micropaleontology 31:82–91.

HASLE, G. R., P. A. SIMS, AND E. E. SYVERTSEN. 1988. Two recent *Stellarima* species: *S. microtrias* and *S. stellaris* (Bacillariophyceae). Bot. Mar. 31:195–206.

HUSTEDT, F. 1930. Die Kieselalgen Deutschlands, Österreichs und der Schweiz und der Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresbegiete. Die Kryptogamenflora von Deutschland, Österreichs und der Schweiz, L. Rabnhorst, ed. 7:1–920.

JOUSÉ, A. P. 1963. The Bacillariophyta. Osnovi Paleontologii 14:55–151.

MORENO, L. 1990. Morfología y sistemática del género *Coscinodiscus* Ehrenberg (Bacillariophyceae), en el sur del Golfo de México. Tesis Maestría, Facultad de Ciencias, Universidad Nacional Autónoma de México. 113p.

RATTRAY, J. 1889. A revision of the genus *Coscinodiscus* and some allied genera. Proc. R. Soc. Edinburgh 16:449–692.

ROSS, R. AND P. A. SIMS. 1972. The fine structure of the frustule in centric diatoms: a suggested terminology. Br. phycol. J. 7:139–163.

———. 1974. Observations on family and generic limits in the Centrales. Nova Hedwigia, Beih. 45:97–121.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:511–530.

ROUND, F. E. AND D. G. MANN. 1980. *Psammodiscus nitidus* new genus, new combination based on *Coscinodiscus nitidus*. Ann. Bot. 46:367–374.

SANCETTA, C. 1987. Three species of *Coscinodiscus* Ehrenberg from north Pacific sediments examined in the light and scanning electron microscopes. Micropaleontology 33:230–241.

SCHRADER, H. 1976. Cenozoic planktonic diatom biostratigraphy of the southern Pacific Ocean. Init. Repts. Deep Sea Drilling Project 35:605–671.

SIMONSEN, R. 1974. The diatom plankton of the Indian Ocean expedition of the R.V. "Meteor", 1964–1965. "Meteor" Forsch.-Ergeb. Reihe D. 19:1–107.

VAN DER WURFF, A. AND H. HULS. 1957–1974. *Diatomeeënflora van Nederland*. O. Koeltz, Koenigstein.

Explanation of Plates

FIGURE LEGENDS: The following abbreviations apply to all figures: BF = brightfield microscopy; PhC = phase contrast microscopy; SEM = scanning electron microscopy. Legends include sample numbers from which observations were made.

Plate 1, Figures 1–11

FIGURE 1. *Coscinodiscus perforatus* var. *cellulosa*, PhC. Sample C-71-18-30B/399. Note radial rows of areolae. Large arrows indicate macrorimoportula notch. FIGURES 2, 3. *C. perforatus* var. *pavillardi*. FIGURE 2. Sample OGI-E47-6-R4/42PI. BF. Small arrows show rimoportulae, large arrows show macrorimoportulae notches. Note radial rows of areolae and locular walls. FIGURE 3. Sample OGI-E48-1-R19/42. PhC. Small arrows indicate rimoportulae on valve face, large arrows show macrorimoportulae notches. FIGURE 4. *C. radiatus*, PhC. Sample OGI-E21-1-R14/4. Arrows show macrorimoportulae notches. FIGURES 5–11. *C. perforatus* var. *cellulosa*, SEM. FIGURE 5. Sample C-71-04-E49A/1191, internal view with outside arrows indicating marginal rimoportulae, inside small arrows showing rimoportulae on valve face, outside large arrows indicate macrorimoportulae. Note radial rows of areolae. FIGURE 6. Sample AH-16E/2303. Arrow shows eccentric rimoportula. FIGURE 7. Sample C-71-04-E49A/1195. Arrow shows macrorimoportula, small arrowheads indicate position of suture cribra filament-siliceous circular bridge, medium arrowhead shows mantle cribra, and large arrowhead indicates submarginal foramina. FIGURE 8. Sample C-71-04-E49A/1196. Arrows show marginal rimoportula, small arrowheads show locular walls, large arrowhead shows marginal foramen. FIGURE 9. Sample AH-16E/2952. External view with arrow indicating macrorimoportula notch. Note radial rows of areolae. FIGURE 10. Sample AH-16E/2313. Arrows show external aperture of rimoportulae, small arrowheads show cribra, medium arrowhead indicates position of eccentric small hole, large arrowhead indicates central area. FIGURE 11. Sample AH-16E/2324. External view with large arrow showing external aperture of macrorimoportula. Note external cribra and suture cribra filaments/siliceous circular bridge. FIGURES 1–5, 9 scale bars = 10 μm; FIGURES 6–8, 10, 11 scale bars = 1 μm.

Plate 2, Figures 12–21

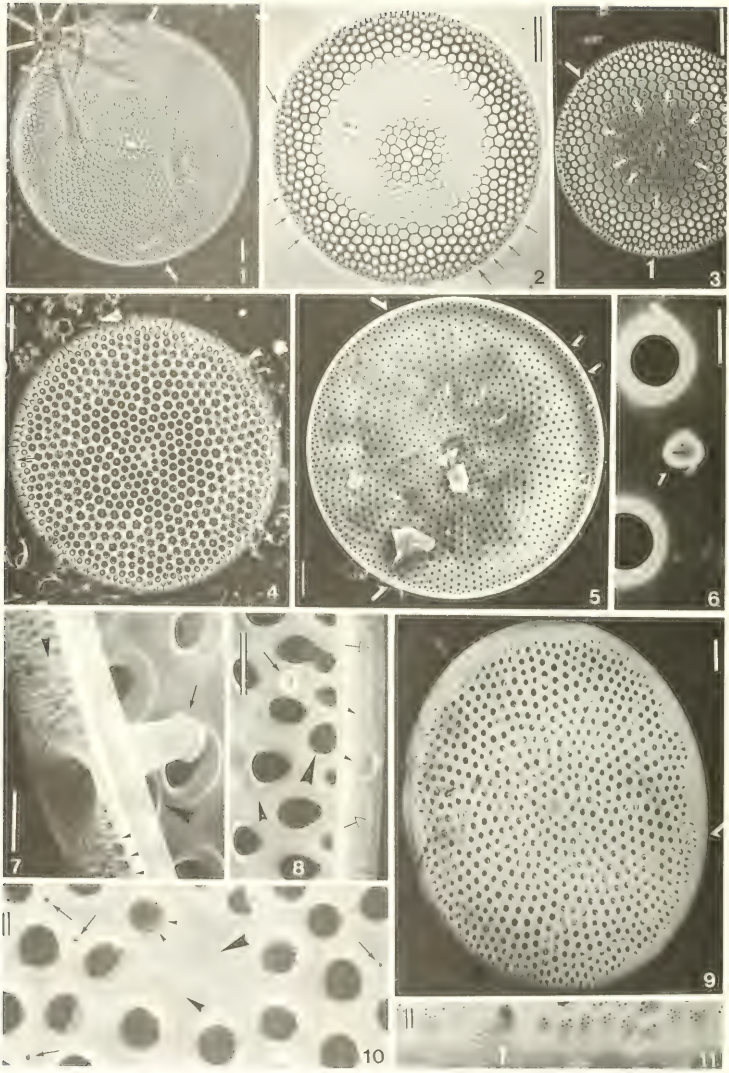
FIGURES 12–21. *C. perforatus* var. *pavillardi*, SEM. FIGURE 12. Sample C-71-04-E49B/1093. Internal view, with outer small arrows indicating marginal rimoportulae, inner arrows indicating eccentric rimoportulae, and large arrows showing macrorimoportulae. Note radial rows of areolae. FIGURE 13. Sample C-71-04-E49B/1094. Small arrow shows pentagonal locular wall, medium arrow shows hexagonal locular wall, and large arrow shows heptagonal locular wall. Note eccentric foramina, rosette with five loculi, and external vela in foramina. FIGURE 14. Sample C71-04-E49B/1089-18. Arrows indicate interlocular rimoportulae. FIGURE 15. Sample C-71-04-E49B/1090-8. Inner arrows show marginal rimoportulae, arrowheads show marks of locular walls/siliceous circular bridge, and triangle arrows show marks of suture filaments. FIGURE 16. Sample C-71-04-E49B/1092. White arrow indicates external aperture of macrorimoportula, black arrow shows tubular rimoportula, triangle arrows show marginal suture filaments/siliceous circular bridge, and arrowheads show locular walls. FIGURE 17. Sample C-71-04-E49B/1091. Small arrow indicates marginal rimoportula, large arrows show flattened apex of rimoprotulae, triangle arrows show suture filament marks, and arrowheads show locular walls. FIGURE 18. Sample C-71-04-E49A/1207. External view with small arrows showing rimoportulae, large arrows indicating macrorimoportulae. FIGURE 19. Sample C-71-04-E49A/1209. Small arrows show marginal rimoportulae, large arrows show external aperture of macrorimoportulae, small arrowhead shows copula, large arrowhead shows valvocopula. FIGURES 20, 21. Samples OGI-58-6/2967,2969, respectively. Specimens tilted 35°, with medium arrowhead indicating pleura, large arrowhead indicating copula, and small arrowhead showing valvocopula. FIGURES 12, 18 scale bars = 10 μm; FIGURES 13–17, 19–21 scale bars = 1 μm.

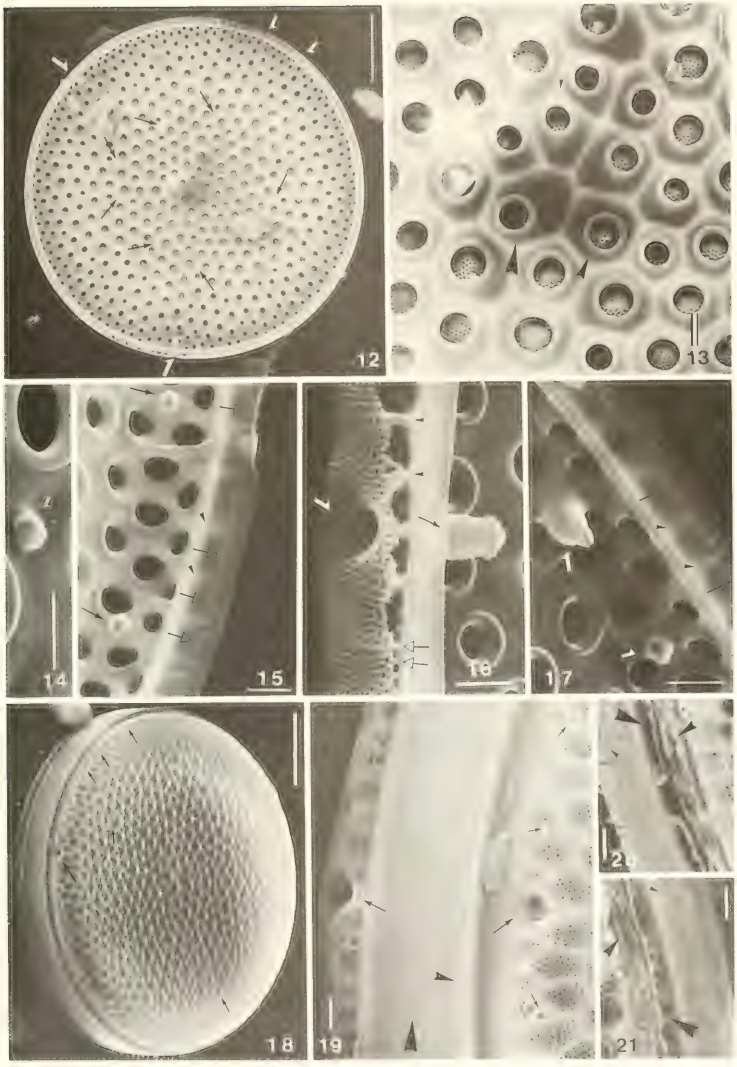
Plate 3, Figures 22–33

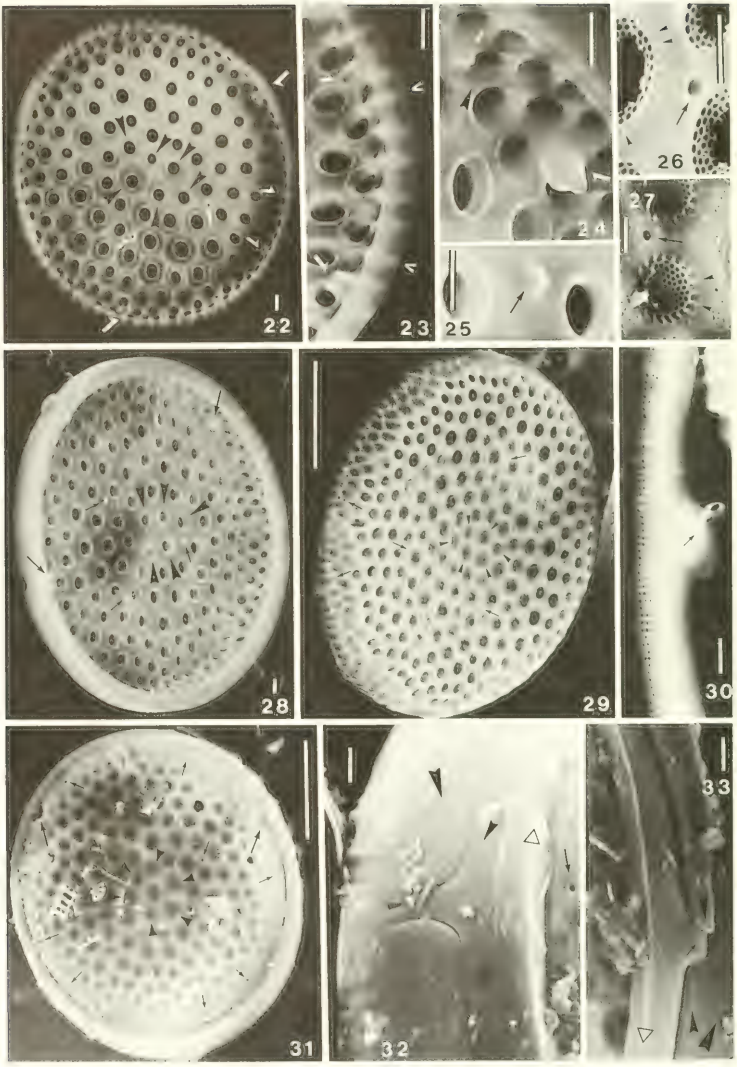
FIGURES 22–33 *C. radiatus*, SEM. FIGURE 22. Sample OGI-E36-2/1695. Internal valve view, with small arrows showing rimoportulae and large arrows showing macrorimoportulae. Arrowheads show rosette formed by six areolae. FIGURE 23. Sample OGI-E36-2/1699. Internal view of margin with small arrows indicating rimoportulae, large arrows show macrorimoportulae, and arrowheads show loculate walls. FIGURE 24. Sample C-71-04-E49B/1112. Internal view, small arrow indicates marginal rimoportula, large arrow shows macrorimoportula, and arrowhead indicates margin-mantle junction. FIGURE 25. Sample C-71-04-E49B/1111. Internal view with arrow indicating interlocular rimoportula. FIGURE 26. Sample C-71-04-E49B/1002. External view with arrow showing aperture of rimoportula on valve face and arrowheads indicating cribra suture filaments. FIGURE 27. Sample AH-16-11/3401. External view of specimen tilted 25° with arrow showing rimoportula aperture and arrowheads indicating cribra suture filaments. FIGURE 28. Sample C-71-04-E49B/1110. Internal view with small arrows showing interlocular rimoportulae, large arrows showing macrorimoportulae, and arrowheads showing eccentric foramina and rosette with six areolae. FIGURE 29. Sample C-71-04-E30B/1000. External view with arrows indicating rimoportulae, arrowheads showing central rosette with six areolae. FIGURE 30. Sample AH-16-11/3033. Arrow shows pleura with ligula. FIGURE 31. Sample AH-16-12/29962. External view with small arrows showing openings of rimoportulae, large arrows showing aperture of macrorimoportulae, and arrowheads showing areolae surrounding one central areola. FIGURE 32. Sample AH-16-12/3018, Specimen tilted 45° with arrow showing external apertures of mantle rimoportula, triangle showing pleura, medium arrowhead showing copula with ligula, and large arrowhead showing valvocopula. FIGURE 33. Sample AH-16-12/30177. Specimen tilted 45°, with triangle showing pleura, arrow showing pleura with ligula, medium arrowhead showing open copula, and large arrow showing valvocopula. FIGURES 22–28, 30, 32, 33 scale bars = 1 μm. FIGURES 29, 31 scale bars = 10 μm.

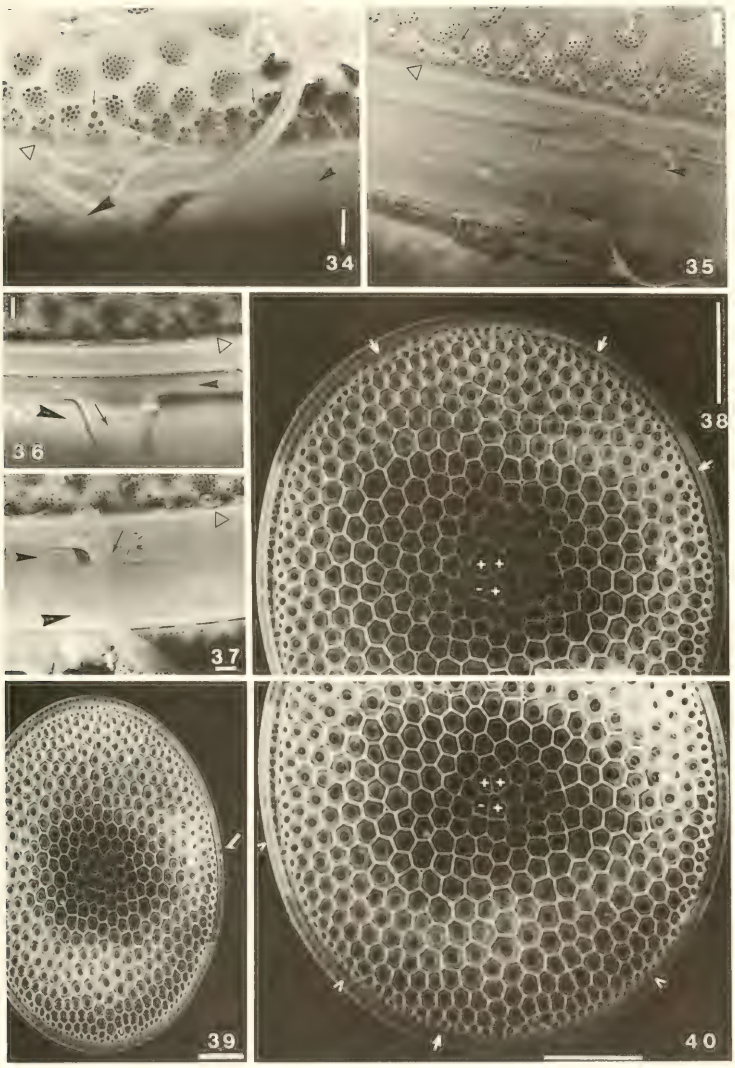
Plate 4, Figures 34–40

FIGURES 34–40. *C. radiatus*, SEM. FIGURES 34, 35. Samples AH-16-11/3021, 3020, respectively. Specimens tilted 35°, external views, with arrows indicating apertures of mantle rimoportulae, triangle indicating pleura, medium arrowhead showing copula with ligula, and large arrowhead showing open valvocopula. Note fine pores on the three bands. FIGURE 36. Sample AH-16-11/3038. Exterior of specimen tilted 35° with triangle showing pleura, medium arrowhead showing copula with ligula (arrow), and large arrowhead showing open valvocopula. FIGURE 37. Sample AH-16- 11/3036. Exterior of specimen tilted 35°, with triangle showing pleura with ligula (arrow), medium arrowhead showing open copula, and large arrowhead showing valvocopula. FIGURES 38, 40. Samples OGI-102-6/2978, 2977, respectively. "-" indicates locular walls with five sides, "+" indicates locular walls with six sides. Arrows indicate secondary radial rows of areolae originating from a five-sided areola and arrowheads show secondary radial rows of areolae originating from six-sided areola. FIGURE 39. Sample OGI-102-6/2976. Arrow showing external aperture of macrorimoportulae. FIGURES 34–37 scale bars = 1 μm; Figures 38–40 scale bars = 10 μm.


1
2
3
4
5
6
7
8
9
10
11


12
13
14
15
16
17
18
19
21


22
23
24
25
26
27
28
29
30
31
32
33


34
35
36
37
38
39
40

Two New Species of the Genus *Surirella* From Lake Turkana, East Africa

by

Erwin Reichardt

Bubenheim 136, D-91757 Treuchtlingen, Germany

with 2 plates

Abstract: Two new species of the genus *Surirella* from Lake Turkana, East Africa, are described using light and scanning electron microscopy. *Surirella turkanensis* is a typical species of the group "Robustae." It is characterized by its narrow, lanceolate shape. The most interesting feature of the second species, *Surirella schuwerkii*, is the partly branched alar canals. These species are compared with morphologically similar congeners.

Introduction

During various studies of different diatom materials, conspicuous or interesting diatoms are found that often must be considered as new species. In this paper, two such diatoms of the genus *Surirella* are considered and described.

Materials and Methods

The material, a bottom sample from Lake Turkana near Ferguson Gulf, was collected by R. and H. Schuwerk on Jan. 3, 1987. Material was acid-cleaned according to standard techniques and embedded into Naphrax for light microscopic (LM) observations. For scanning electron microscopy (SEM), valves were selected by hand under the LM and mounted onto cover glasses with gelatin. In general, the method follows the description of Hustedt (1929) for making slides with single specimens. The selection of rare but relatively robust diatoms under the LM is rather simple and much faster than the time-consuming and often unsuccessful or ineffective searching in the SEM. In addition, the position of the valves or frustules can be determined and valves can be selectively broken for morphological studies.

Results and Discussion

Surirella turkanensis, n. sp.

Descriptio: Frustula isopolaria. Valvae anguste lanceolatae apicibus acutis fere subprotractis, 142–255 µm longae, 21.5–32.5 µm latae. Canales alares 16–22 in 100 µm, projectione alarum perspicua. Superficies valvarum distincte undulata, undulis lineam mediam attingentibus, depressionibus cum structuris irregularibus silicis. Striae transapicales delicatae, 25–32 in 10 µm.

Holotypus: Sub no. S784-T01 in collectione Reichardt.

Isotypus: Sub no. Zu4/2 in collectione Bremerhaven (BRM).

Description: Frustules isopolar about apical axis. Valves narrowly lanceolate with acute and mostly somewhat protracted ends, 142–255 µm long, 21.5–32.5 µm wide. Wing canals 16–22 in 100 µm, wing projection clear. Transapical waves distinct, reaching the middle line, wave troughs with irregular siliceous structures. Cell wall with fine transapical striae, 25–32 in 10 µm.

Type locality: Lake Turkana, East Africa.

Comments: *Surirella turkanensis* has all of the features of the group Robustae (cf. Krammer 1989), including marked alae and alar canals or areolae that are distributed over the entire valve surface. It is characterized especially by its narrowly lanceolate shape. The only species similar to *S. turkanensis* is *Surirella nipponica* Skvortzow. This species, however, is not well known (the descriptions in Skvortzow 1936a and 1936b differ in some points) and it is distinguished by its more obtusely rounded poles, smaller size, distinct striae, and lack of irregular structures in the wave troughs.

The new species was previously reported by Gasse (1986, p. 173, Pl. XL, Figs. 1–5) as "*Surirella* sp. 1" from nearly the same sampling point (Lake Turkana, Ferguson Gulf). The breadth of this species given by Gasse (60–70 µm; p. 173) must be a mistake since dimensions in her micrographs agree entirely with my specimens. Specimens were epiphytized by other diatoms, especially *Navicula damasii* Hust. (Fig. 6), a phenomenon reported also by Gasse (1986).

Surirella schuwerkii, n. sp.

Descriptio: Valvae heteropolares, late ovatae, polo ad capitulum late rotundato, polo ad pedem angustiore cuneato obtuso, 61.5–96 µm longae, 38–61 µm latae. Superficies valvarum in media parte distincte undulata, undulis parallelibus vel subradiantibus quae in lineam in medio elevatam transeunt quae linea polos non attingit. Undulae circa polos quasi planae. Canales alares ex quadam parte ramosae portulis semel vel binis vel ternis in canalem raphis influentes. Superficies varvarum tota irregularibus granulis affecta.

Holotypus: Sub no. S784-T02 in collectione Reichardt.

Isotypus: Sub no. Zu4/2 in collectione Bremerhaven (BRM).

Description: Valves heteropolar, broadly ovate, head pole broadly rounded, foot pole narrower and cuneate obtuse, 61.5–96 µm long, 38–61 µm wide. Transapical waves distinct in the middle part of the valve, parallel to slightly radiate, running into a distinct median elevation that does not reach the poles. Waves at both poles flattened. Wing canals partly branched with 1–3 portulae to the raphe canal. Entire valve surface randomly studded with conspicuous granules.

Type locality: Lake Turkana, East Africa.

Comments: *Surirella schuwerkii* shows a more interesting and complex structure than *S. turkanensis*. The most striking features are the partially branched alar canals that are also present but much more developed in the brackish marine diatom *S. striatula* Turpin. Other species with branched alar canals, including *S. anassae* Cholnoky, *S. bengalensis* Grunow, *S. dumae* Hustedt, *S. fluvicygnorum* John, *S. guyanensis* H. Peragallo, *S. inducta* A. Schmidt and "*S.* sp." in Negoro and Gotoh (1983, Fig. 271), are clearly differentiated from *S. schuwerkii* by the structure of the valve surfaces. A very similar species, *S.*

kapitiana, was described in detail by Stidolph (1985). As his description and SEM micrographs show, *S. kapitiana* possesses principally the same morphological construction as *S. schuwerkii*. It is distinguished, however, by the larger areolae of the cell wall and the much smaller granules on the outer valve surface. A nipple-like process situated on the valve interior of *S. kapitiana* has not been detected in *S. schuwerkii*. Foged (1979, Pl. XLV, fig. 6) depicts a *Surirella*, identified by Foged as *S. robusta* f. *lata* Hust. which, as far as is discernible from the micrograph, shows the characteristics of *S. schuwerkii*.

Acknowledgements

I would like to thank R. and H. Schuwerk for collecting many diatom materials from East Africa and W. Klose for helping with the Latin diagnoses and the English script.

Literature Cited

FOGED, N. 1979. Diatoms in New Zealand, The North Island. Bibl. Phycologia 47:1–225.

GASSE, F. 1986. East African diatoms. Taxonomy, ecological distribution. Bibl. Diatomologica 11:1–201.

HUSTEDT, F. 1929. Vom Sammeln und Präparieren der Kieselalgen sowie Angaben über Untersuchungs- und Kulturmethoden. Pp. 1–99 *in* Handbuch der biologischen Arbeitsmethoden, E. Abderhalden, ed. Urban & Schwarzenberg, Berlin and Wien.

KRAMMER, K. 1989. Functional valve morphology in some *Surirella* species (Bacillariophyceae) and a comparison with the Naviculaceae. J. Phycol. 25:159–167.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae. Teil 2, Bacillariaceae, Epithemiaceae, Surirellaceae. H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. *Süßwasserflora von Mitteleuropa*, Bd. 2, Teil 2. Gustav Fischer, Jena

NEGORO, K. AND T. GOTOH. 1983. Diatom Vegetation of the River Yura. Mem. Fac. Agr. Kinki Univ. 6:67–118.

SCHMIDT, A., ET AL. 1874–1959. Atlas der Diatomaceenkunde. R. Reisland, Leipzig.

SKVORTZOW, B. W. 1936a. Diatoms from Kizaki Lake, Honshu Island, Nippon. Philippine J. Sci. 61:9–73.

———. 1936b. Diatoms from Biwa Lake, Honshu Island, Nippon. Philippine J. Sci. 61:253–296.

STIDOLPH, S. R. 1985. Some benthic diatoms from Kapiti Island, near Cook Strait, New Zealand. Nova Hedwigia 41:393–415.

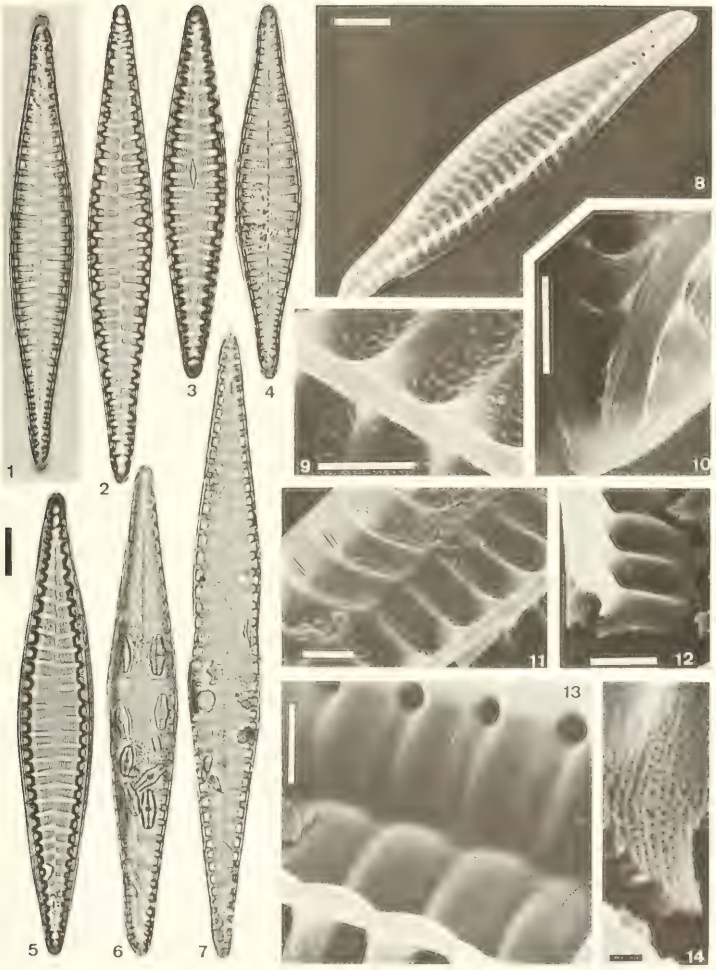
Explanation of Plates

Plate 1, Figures 1–14

FIGURES 1–14. *Surirella turkanensis*, n. sp. FIGURES 1–7. LM. FIGURE 1. Holotype specimen. FIGURE 6. Specimen with epiphytic diatoms (*Navicula damasii*). FIGURE 7. Longer valve showing a very faint constriction in the middle. FIGURES 8–14. SEM. FIGURE 8. Valve exterior. FIGURE 9. Wing with raphe fissure. FIGURE 10. Interruption of raphe at valve pole. FIGURE 11. External view of valve surface showing alae, barred fenestrae, waves, and random siliceous structures on wave troughs. FIGURE 12. Inside view of a transapically broken valve with cross section of raphe canal. FIGURE 13. Valve interior. FIGURE 14. Valve interior showing small areolae. Scale bars: FIGURES 1–8 = 20 μm, FIGURES 9–13 = 5 μm, FIGURE 14 = 1 μm.

Plate 2, Figures 15–26

FIGURES 15–26. *Surirella schuwerkii*, n. sp. FIGURES 15–19. LM. FIGURE 15. Holotype specimen. FIGURE 19. Valve margin showing branched alar canals. FIGURES 20–26. SEM. FIGURE 20. Valve exterior. FIGURE 21. Valve exterior seen from the footpole. FIGURE 22. Valve exterior showing interruption of raphe fissure. FIGURE 23. Cross section of alar canal showing it is transversely widened but not branched. The raphe canal is partially broken off. FIGURE 24. Branched alar canals. FIGURE 25. Valve interior. FIGURE 26. Internal view of alar canals with openings (portulae) into the raphe canal. Scale bars: FIGURES 15–18 = 20 μm, FIGURE 19 = 10 μm (black bar), FIGURES 20–21, 24–26 = 5 μm, FIGURES 22–23 = 1 μm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14

15

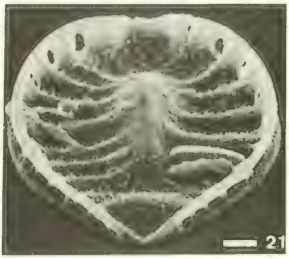
16

17

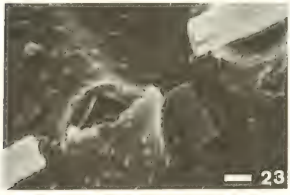
18

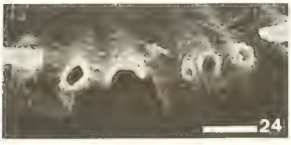
19

20


21

22


23


24

25

26

Do Diatom "Superspecies" Ever Evolve?

by

Susan Soltau Kilham

Department of Biology, University of Michigan, Ann Arbor, Michigan 48109-1048[1]

with 2 figures

Abstract: Previous studies on the physiological ecology of planktonic diatoms showed trade-offs in the ability of species to compete for essential resources. (For example, araphid diatoms grow well at high Si:P supply ratios (excellent competitors for P, but requiring relatively high Si levels), while some centric diatoms compete best at low Si:P ratios.) Do "superspecies" ever evolve that compete well for both nutrients? This may occur when new habitats appear, but such situations are inherently unstable. At the beginning of the Pleistocene a new habitat type appeared: many low phosphorus lakes created by glaciation events. Prior to that period, lakes were large, deep, probably low in silicon, and dominated by centric diatoms in the genera *Stephanodiscus* and *Cyclotella*. Existing araphid diatoms exploited the new low P (high Si:P) environments, in effect acting as "superspecies." The evolution of new species was the result of selection through nutrient competition for organisms to exploit the broad Si:P ratio gradient. If this scenario occurred in freshwater lakes, the extant araphid planktonic species in freshwater should be genetically more closely related to each other than they are to their marine congeners. Similarities in shape between marine and freshwater araphids may be convergence of form in the planktonic environment. Modern molecular techniques allow testing of this hypothesis, both in the degree of similarity between freshwater and marine congeners and in the timing of such events.

Introduction

Diatom biologists often express a desire for links among various aspects of the physiology, ecology, evolution, and systematics of diatoms (Round 1984; Bradbury 1986). I offer a highly speculative example of such an integration, based on physiological attributes of some freshwater planktonic araphid species and the possible selection processes that arose during the Pleistocene and may have increased the diversity of diatom communities. Some physiological traits may be quite characteristic of groups of species. Using these traits within an ecological framework may help us to understand many aspects of their biology.

Resource Ratios

We have learned a great deal about the physiological characteristics of a modest number of freshwater planktonic diatom species in the past 20 years that have led to insights about their distributions and relative abundances (Kilham 1971; Tilman 1982; Tilman et

[1]Current address: Department of Biosciences and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104.

al. 1982; Kilham 1986; Reynolds 1984; Sommer 1988). One of the conclusions is that resource ratio gradients are important in structuring diatom communities, both in freshwater and marine environments (Sommer 1986). The mechanism causing this structuring process is related to the physiological tradeoffs that species show in their abilities to grow and compete along such gradients.

One frequently asked question, first posed to me by G. E. Hutchinson in 1977, is: Do superspecies ever evolve that are good competitors for a number of resources? Tilman (1982) addressed this question to some degree, and I will expand those general arguments here. In general, Tilman argued that any phenotypic heterogeneity in competitive ability within a newly arisen "superspecies" will tend to decrease if there is a cost to maintaining competitive ability for the "non-limiting" resource within a particular resource habitat. The degree of heterogeneity in resource supply ratios is an important consideration. Phenotypic diversity would be favored in very heterogeneous environments.

One clue that there are costs to maintaining competitive ability for non-limiting resources is seen in the relative abilities of *Asterionella formosa*, *Fragilaria crotonensis* and *Stephanodiscus hantzschii* to grow under silicon (Si) or phosphorus (P) limitation over a range of temperatures (van Donk and Kilham 1990). The two araphid species have very low, narrow, and constant half-saturation growth constants (Ks) for P, but high and variable Ks values for Si. These two species are good competitors for P, but poor competitors for Si. The opposite is true for *S. hantzschii*, which has low, narrow, and constant Ks values for Si and high, variable values for P, and is an excellent competitor for Si (see also Kilham 1984). These tradeoffs suggest that there is a cost to maintaining competitive ability (i.e., a low Ks for growth) for all potentially limiting resources simultaneously. Some aspects of physiological ability can be a species-specific characteristic.

The importance of trade-offs in physiological characteristics of species has generated hypotheses about physiological adaptation in African diatom species that are consistent with their modern and recent fossil distributions (Kilham et al. 1986; P. Kilham and S. S. Kilham 1990; S. S. Kilham and P. Kilham 1990). Centric and monoraphid diatoms tend to dominate diatom communities in tropical lakes, while araphid diatoms frequently dominate in temperate lakes. Lake size is a complicating factor. In the tropics, small lakes tend to have high Si:P ratios (usually dominated by araphid species in the genus *Synedra*) and large lakes have low Si:P ratios (P. Kilham and S. S. Kilham 1990; S. S. Kilham and P. Kilham 1990), perhaps because organisms control the nutrient cycles. The picture is complicated in the temperate zone because of the large fluctuations of light and temperature that increase physical and geochemical dominance of nutrient cycling, but the generalization can still be made that small (undisturbed) lakes frequently have high Si:P ratios, with accompanying dominance by araphid diatoms (see Figure 1A).

The next problem to address is just how variable resources can be within a lake or among lakes. A few generalizations will be attempted. It seems likely that heterogeneity in supply ratios of resources will likely be greater in any particular lake in the temperate zone than in the tropics because resources can accumulate in the winter when low light and temperature keep phytoplankton production low. It may be that lake size and water retention time are factors that make large lakes less variable in supply ratios than small lakes. Trophic state is also a factor affecting supply ratios, with oligotrophic lakes being less variable than eutrophic lakes (at least in the temperate zone). Lovstad and Bjorndalen (1990) showed that consumption rates of N and Si tended to be constant over the growing season within a lake in Norway and were related to the initial P level among lakes.

PLEISTOCENE "SUPERSPECIES"?

The above discussion leads to the speculation that, prior to the Pleistocene glaciation events, lakes tended to be large, to have low Si:P ratios, and therefore to be dominated by centric diatoms. I am proposing that in the Pleistocene, high Si:P ratio lakes became much more abundant because of the creation of many small, oligotrophic, temperate lakes with high Si:P ratios. This environment was ideal for exploitation by araphid diatoms in the family Fragilariaceae (Figure 1).

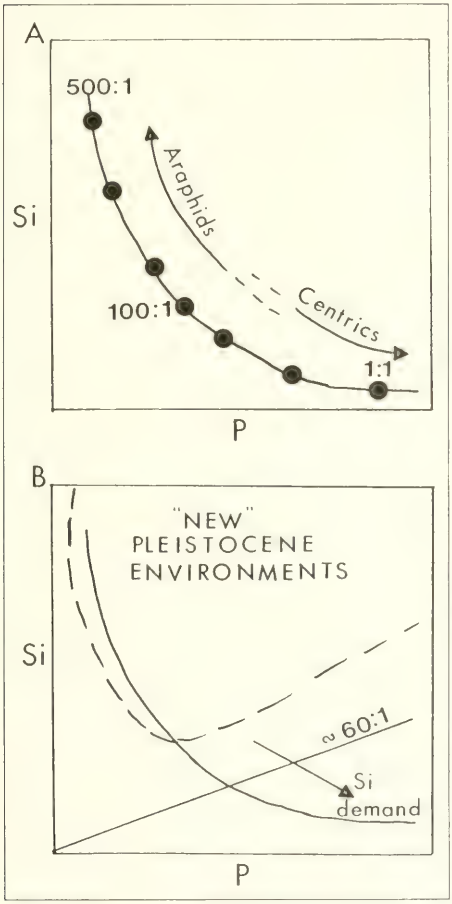


FIGURE 1. A. Si:P tradeoff curve for diatoms (dots) illustrating the general domains of dominance by freshwater planktonic araphid and centric diatoms. Representative Si:P atomic ratios are provided for scale. B. Hypothesized region of Si:P supply ratios in new lakes appearing in the Pleistocene owing to glaciation events. The 60:1 ratio line represents the "average world river Si:P ratio" (see Kilham and Kilham 1990). The Si demand arrow shows the tendency for ratios to decrease owing to biogeochemical factors, especially consumption by diatoms and lower recycling rates of Si.

Araphid diatoms are frequently abundant in small, clear streams, which may have high Si:P ratios. I am proposing that the appearance of many high Si:P lakes provided a new planktonic niche for some species that may have already been good at growing at very low phosphorus levels in streams. Early colonizers of these lakes would be "superspecies" to the degree that Si limitation was relieved and competition for P would be the rule over a broad range of Si:P supplies. Certain adaptations for life in the plankton were easily available, such as the long, slender cells of *Synedra*, and the grazing resistant colonial forms of *Asterionella*, *Fragilaria*, and *Diatoma*. As discussed above, phenotypic heterogeneity within the putative "superspecies" would be likely to decrease within particular lakes because of the cost of maintaining competitive ability for the non-limiting resource. The wide range of moderate to high Si:P supply ratios among the available lakes should lead to species segregation. Modern representatives in these genera are arrayed along an Si:P ratio gradient in competitive ability (see above), perhaps as a result of dividing up the gradient through selection by nutrient competition and reduction of grazing losses.

These arguments generate the hypothesis that the planktonic freshwater Fragilariaceae should be more closely related to each other than to their marine congeners and that speciation has been rapid during the Pleistocene and Recent epochs among species in the freshwater genera. There have been several recent papers about the systematics of the Fragilariaceae that support the idea that the freshwater and marine representatives previously assigned to the genera *Fragilaria* and *Synedra* might be much more diverse than previously supposed (Figure 2). Reid and Round (1987) said, "There are great taxonomic problems amongst the linear araphid genera both of freshwater and marine habitats; few, if any marine species, belong in *Synedra* sensu stricto" (p. 219). Similarities in morphology may be due in part to convergence of form in a planktonic environment (Round 1984).

Testing of this hypothesis is possible with modern molecular techniques employing DNA homologies. Diatom chloroplast DNA is likely to be a good choice for distinguishing among species within a family. Newly developed methods using the polymerase chain reaction (PCR) make this a feasible proposition. The degree of genetic similarity among planktonic species in freshwater and marine environments as well as the relative timing of speciation events may all be possible to document.

Other Examples

There may be other environmentally related changes that allow links to be made between physiological characteristics and the evolution and systematics of diatoms.

The genus *Asterionella* in freshwater does not have a large number of species. *Asterionella formosa* Hass. is characteristic of habitats with moderate Si:P ratios (Kilham et al. 1982; van Donk and Kilham 1990). *Asterionella ralfsii* var. *americana* Korn is an indicator of acidification because it occurs in nature at pH levels below those usually tolerated by planktonic diatoms (ca. pH 6; Charles 1985). This may be a further, relatively recent event in the speciation of freshwater planktonic Fragilariaceae in response to the increase the number of acidic lakes. Gensemer (1990) has shown that two characteristic morphologies (long-form and short-form) occur within a clone (UTCC #170) under varying aluminum levels. The short form is more characteristic at high Al concentrations. It is only in the last few decades that increasing acidity of the rain has caused increased Al levels to be more frequent in lakes below pH 6. A field study of the occurrence and genetic similarity of these different forms, along with Si, P, and Al chemistry, might detect some segregation among these morphotypes that could be ascribed to environmental conditions.

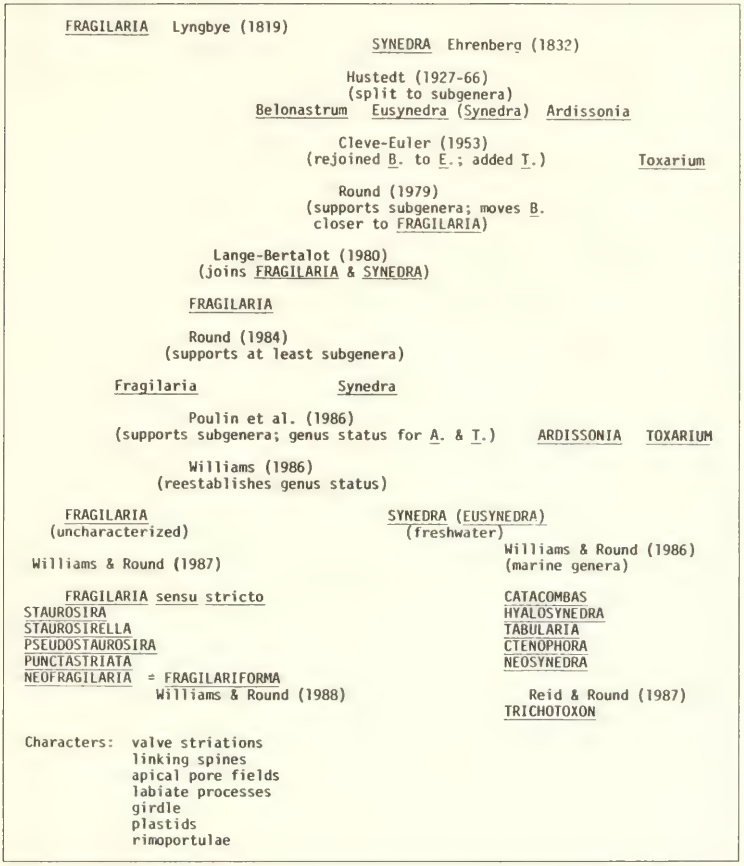


FIGURE 2. A taxonomic summary for the genera *Fragilaria* and *Synedra*. Names with all capitals indicate genus; names with lower case indicate subgenus. Attention is called to the separation of freshwater species to the genus *Synedra* and the marine species to several new genera (lower right). The major characteristics used to distinguish the present genera are listed in the lower left. References prior to 1986 can be found in Poulin et al. (1986).

The genus *Melosira* (*Aulacoseira*) is an ancient and species rich group in freshwater. Kilham (1990) recently reviewed the ecology of species within this genus, especially for Africa. He expanded upon the hypothesis that a light:P tradeoff curve might be a selective force (Kilham et al. 1986). This observation is supported by the fact that the pore size variation among species follows the light:P tradeoff curve. African lakes have a wide range of light environments, including lakes with mixing depths in excess of 100 m (ex-

tremely low light) but moderate P levels (low light:P ratios). Examination of physiological abilities along with morphological and genetic relatedness among species along this trade-off curve might also be a source of information to make links from the physiological to the systematic and paleontological levels.

Acknowledgements

I greatly valued early discussions on this problem with Peter Kilham, David Tilman, and Robert Guillard. Jeffrey Palmer tutored me in the usefulness of applying chloroplast DNA techniques and advised waiting "until techniques catch up to the question" to actually test it. I am grateful to James Cotner and Robert Gensemer for editorial suggestions. This paper is dedicated to G. E. Hutchinson and P. Kilham.

Literature Cited

BRADBURY, J. P. 1986. Continental diatom biostratigraphy and paleolimnology. Pp. 667–686 *in* Proceedings of the Eighth International Diatom Symposium, M. Richard, ed. O. Koeltz, Koenigstein.

CHARLES, D. F. 1985. Relationships between surface diatom assemblages and lakewater characterisitcs in Adirondack lakes. Ecology 66:994–1011.

GENSEMER, R. W. 1990. Role of aluminum and growth rate on changes in cell size and silica content of silica-limited populations of *Asterionella ralfsii* var. *americana* (Bacillariophyceae). J. Phycol. 26:250–258.

KILHAM, P. 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. Limnol. Oceanogr. 16:10–18.

———. 1990. Ecology of *Melosira* species in the Great Lakes of Africa. Pp. 414–427 *in* Large Lakes: Ecological Structure and Function, M. M. Tilzer and C. Serruya, eds. Springer-Verlag, Berlin.

KILHAM, P., S. S. KILHAM, AND R. E. HECKY. 1986. Hypothesized resource relationships among African planktonic diatoms. Limnol. Oceanogr. 31:1167–1179.

KILHAM, P. AND S. S. KILHAM. 1990. Endless summer: Internal loading processes dominate nutrient cycling in tropical lakes. Freshw. Biol. 23:379–389.

KILHAM, S. S. 1984. Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. Int. Ver. Theor. Angew. Limnol. Verh. 22:435–439.

———. 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient. Can. J. Fish. Aq. Sci. 43:351–360.

KILHAM, S. S. AND P. KILHAM. 1990. Tropical limnology: Do African lakes violate the "first law" of limnology? Int. Ver. Theor. Angew. Limnol. Verh. 24:1–5.

POULIN, M., L. BERNARD-THERRIAULT, AND A. CARDINAL. 1986. *Fragilaria* and *Synedra* (Bacillariophyceae): A morphological and ultrastructural approach. Diatom Res. 1:99–112.

REID, F. M. AND F. E. ROUND. 1987. The Antarctic diatom *Synedra reinboldii*: Taxonomy, ecology and transference to a new genus, *Trichotoxon*. Diatom Res. 2:219–227.

REYNOLDS, C. S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge. 384 pp.

ROUND, F. E. 1984. The circumscription of *Synedra* and *Fragilaria* and their subgroupings. Pp. 241–253 *in* Proceedings of the Seventh International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

SOMMER, U. 1986. Nitrate- and silicate-competition among Antarctic phytoplankton. Mar. Biol. 91:345–351.

———. 1988. Growth and survival strategies of planktonic diatoms. Pp. 227–260 *in* Growth and Reproductive Strategies of Freshwater Phytoplankton, C. D. Sandgren, ed. Cambridge University Press, Cambridge.

TILMAN, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton. 296 pp.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: The role of limiting nutrients. Ann. Rev. Ecol. Syst. 13:349–372.

VAN DONK, E. AND S. S. KILHAM. 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. J. Phycol. 26:40–50.

WILLIAMS, D. M. 1985. Morphology, taxonomy and inter-relationships of the ribbed araphid diatoms from the genera *Diatoma* and *Meridion* (Diatomaceae: Bacillariophyta). Bibl. Diatomologica 8:1–238.

———. 1986. Comparative morphology of some species of *Synedra* Ehrenberg with a new definition of the genus. Diatom Res. 1:131–152.

WILLIAMS, D. M. AND F. E. ROUND. 1986. Revision of the genus *Synedra* Ehrenberg Diatom Res. 1:313–339.

———. 1987. Revision of the genus *Fragilaria*. Diatom Res. 2:267–288.

———. 1988. *Fragilariforma*, nom. nov., a new generic name for *Neofragilaria* Williams & Round. Diatom Res. 3:265–267.

Morphological Variability of *Navicula recens* (Lange-Bertalot) Lange-Bertalot

by

H. Fukushima

Tokyo Women's College of Physical Education, Kunitachi, Tokyo, Japan,

T. Kobayashi

Yokohama City University, Seto Kanazawa-ku, Yokohama, Japan,

H. Ohtsuka

Environmental Analysis Inst. Kanagawa, Assoc. Negishi, Yokohama, Japan,

and

S. Yoshitake

Shonan Junior College, Yokosuka, Japan

with 2 figures and 6 plates

Abstract: Morphological variability of *Navicula recens* was studied in a brackish stream population from Okinawa prefecture, Japan. Valves were lanceolate to linear-lanceolate, 21.5–51 µm long, 5.5–7.5 µm broad, with 10–15 striae in 10 µm. Variation was observed in valve margins and apices as well as size and structure of the central area. Relative abundances of the different morphological forms in the population were calculated. Despite the variability in size, outline, and central area, specimens from Japan are similar to those described by Krammer and Lange-Bertalot (1986).

Introduction

Intraspecific variability of diatoms is well documented (e.g., Krammer and Lange-Bertalot 1986), however, intensive studies on population variation have not been widely undertaken. The present study details variation in valve outline, shape of the central area, and angle of striae of *Navicula recens* (Lange-Bertalot) Lange-Bertalot from a brackish stream in Japan.

Materials and Methods

The sample upon which observations were made was taken from a brackish stream, Suguo, in the Okinawa Prefecture, Japan, in April, 1987. Attached epilithic diatoms were collected by scraping, fixed in 10 % formalin, then cleaned by a sulphuric acid and hydrogen peroxide method. Cleaned material was mounted in Pleurax and observations made with light microscopy.

Results

Valves of *N. recens* are lanceolate to linear-lanceolate in shape, 21.5–51 µm long and 5.5–7.5 µm broad. Correlation coefficient for length and breadth was 0.601, a value suggesting a strong relationship between them (Fig. 2). Striae number 10–14/10 µm (mode = 12) at the center of the valve, 12–15/10 µm (mode = 13) near the apices (Figure 1). Puncta density was 30–35/10 µm.

Variation in valve features of *N. recens* included valve outline, shape of the apices, size, symmetry, and shape of the central area, and presence/absence and placement of Voigt faults. Two types of valve margins were identified, convex at the valve center (Plate 1, Figs. A–J) and mostly parallel at the center (Plate 1, Figs. K–T). Relative frequencies of these morphologies were 65 % and 35 %, respectively. Apices of the valve were either slightly acute (Plate 2, Figs. A–J; 89.2 %) or rounded (Plate 1, Figs. U–f; 10.8 %).

Structure of the central area was small (Plate 2, Figs. K–T; 16.6 %) or "standard" (83.4 %). Size of the central area was different between the staff and distaff sides, and in some specimens, three types of central-area symmetry could be identified; expanded central area on the distaff side (Plate 3, Figs. A–I; 14.8 %), large, expanded central area on the staff side (Plate 3, Figs. J–S; 16.1 %), and nearly similar on both sides of the axial area (Plate 3, Figs. T–c; 69.1 %). Shape of the central area could be broken down into five types: nearly rounded (Plate 4, Figs. A–J; 38.0 %), nearly square (Plate 4, Figs. K–T; 8.6 %), rectangular (Plate 4, Figs. U–c; 5.4 %), nearly rhombic (Plate 5, Figs. A–J), and shaped otherwise (Plate 5, Figs. K–T; 11.3 %). Orientation of the striae around the central area was strongly radiate (Plate 6, Figs. 17.9 %) or almost parallel (Plate 6, Figs. U–e; 82.1 %).

Voigt faults were present or absent, and in those valves where a Voigt fault was observed, its placement was variable. Six conditions relative to Voigt faults were identified, and the relative frequencies of these conditions calculated. They include: one Voigt fault at the upper part of the staff side (Plate 5, Figs. U–W; 20.6 %), one Voigt fault at the lower part of the staff side (Plate 5, Figs. X–d; 7.2 %), two Voigt faults with one at the upper part and one at the lower part of the staff side (Plate 6, Figs. A–D; 8.5 %), one Voigt fault at the upper part of the distaff side (1.3 %), one Voigt fault at the lower part of the distaff side (1.3 %), and no Voigt faults (Plate 6, Figs. E–J; 61.1 %).

Discussion

Observations presented here on the morphological variability of *N. recens* are consistent with previously published reports of size, striae densities, and density of puncta (e.g., Krammer and Lange-Bertalot 1986; Reichart 1984; Foged 1984). Specimens from Suguo stream, however, were longer (up to 51 µm) and more narrow (5.5 µm) than previously reported.

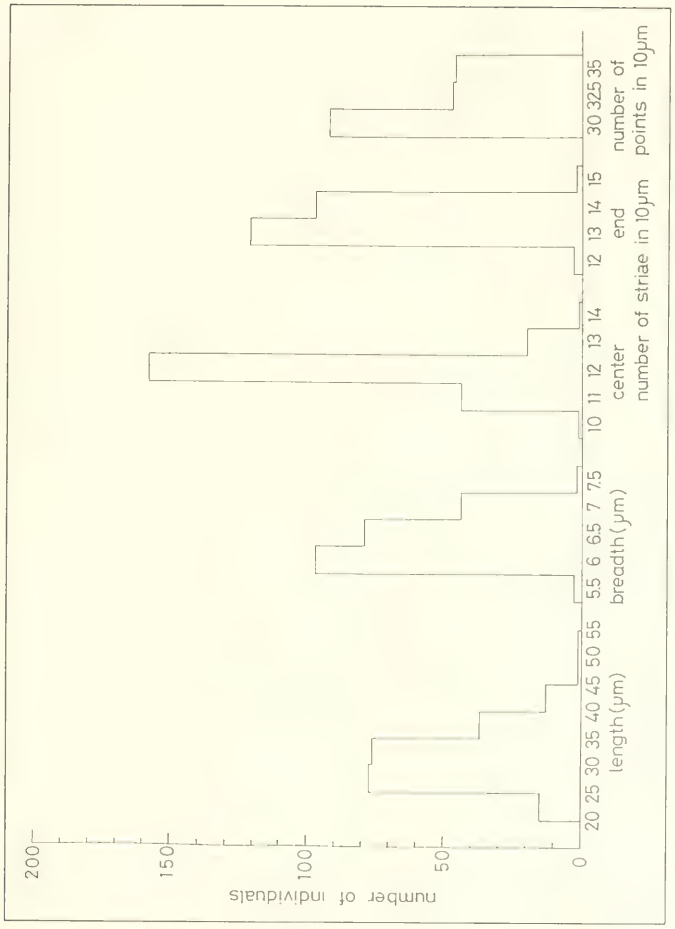


FIGURE 1. *Navicula recens*. Histograms showing number of individuals in each range of length, breadth, and density of the striae and punctuation in 10 μm.

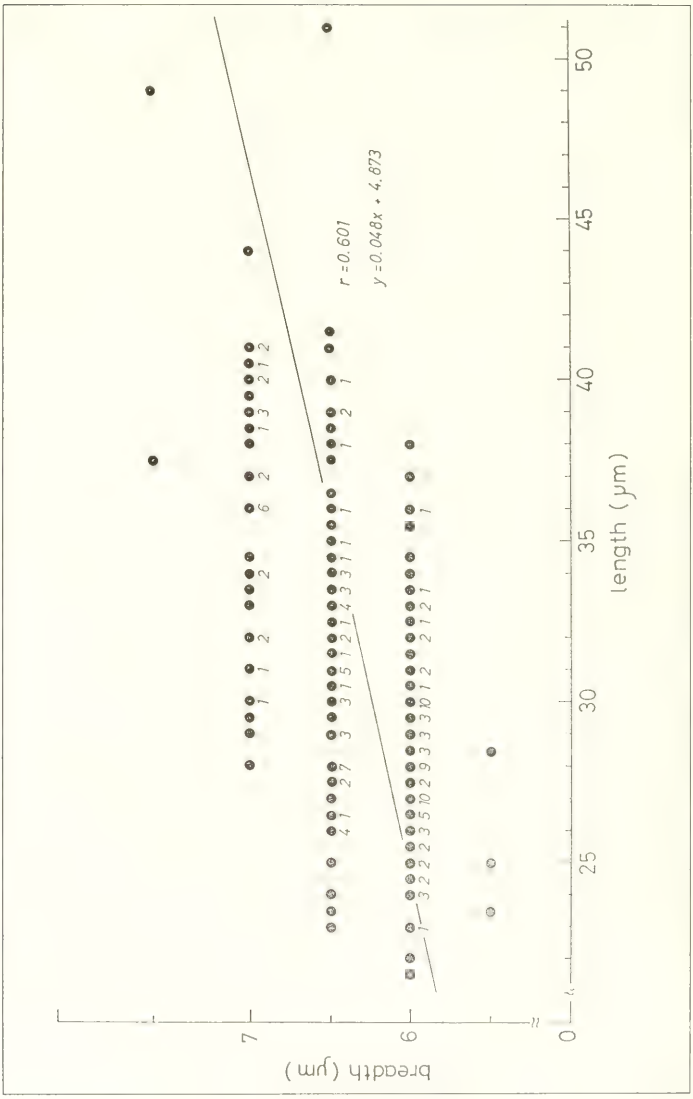


FIGURE 2. *Navicula recens*. Diagrams of the correlation of breadth with length of valve.

In the key to *Navicula* species, Krammer and Lange-Bertalot (1986:93) divided *N. recens* and its close relatives into two groups, those with weakly radiate striae (to which belong *N. tripunctata*, *N. cincta*, *N. veneta*, *N. maralithii*, and *N. recens*) and those with distinctly radiate striae (including *N. angusta*, *N. radiosa*, *N. cryptocephala*, and *N. lanceolata*). Of the specimens observed from Suguo stream, 82.1 % had almost parallel striae and thus would be considered in the first group of Krammer and Lange-Bertalot's. This initial group was further divided into two groups, including those with a linear outline (to which *N. tripunctata* belonged) and those with a linear-lanceolate to lanceolate outline (including *N. cincta*, *N. veneta*, *N. margalithii*, and *N. recens*). Breadth is used to distinguish *N. cincta* and *N. veneta* (breadth less than 6.5 µm) from *N. margalithii* and *N. recens* (breadth greater than 6.5 µm). In our investigation 125 of 230 valves (54.3 %) of *N. recens* were 6.5 µm or greater in breadth, thus conforming to Krammer and Lange-Bertalot's separation. Furthermore, Krammer and Lange-Bertalot distinguished *N. margalithii* from *N. recens* on the basis of striae and puncta densities. They indicate striae and puncta densities of 9–10 µm and 30/10 µm, respectively, for *N. margalithii* and 11–14/10 µm and 35/10 µm, respectively, for *N. recens*. From these data our specimens might be considered as *N. recens*, although they point out some discrepancies in Krammer and Lange-Bertalot's key with respect to valve size and striae orientation.

Krammer and Lange-Bertalot (1986) present five photomicrographs of this species, two of which are considered of uncertain species. Our specimens differ from the figures of Krammer and Lange-Bertalot only in having an equal size of the central area between staff and distaff sides, while the Krammer and Lange-Bertalot specimens possess larger central areas at the staff side. In other respects, however, our specimens agree with the features shown in the figures of Krammer and Lange-Bertalot.

Literature Cited

FOGED, N. 1984. Freshwater and littoral diatoms from Cuba. Bibl. Diatomologica 5:1–243.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Naviculaceae. Volume 2, Part 1. *In* Süsswasserflora von Mitteleuropa. Bacillariophyceae, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fisher, Stuttgart. 876p.

REICHARDT, E. 1984. Die Diatomeen der Altmühl. Bibl. Diatomologica 6:1-167.

Explanation of Plates

Plate 1, Figures A–f
FIGURES A–f. *Navicula recens* (× 2000). FIGURES A–J. Valves with convex margins (65.0 %). FIGURES K–T. Valves with parallel or mostly parallel margins (35.0 %). FIGURES U–f. Valves with slightly rounded apices (10.8 %).

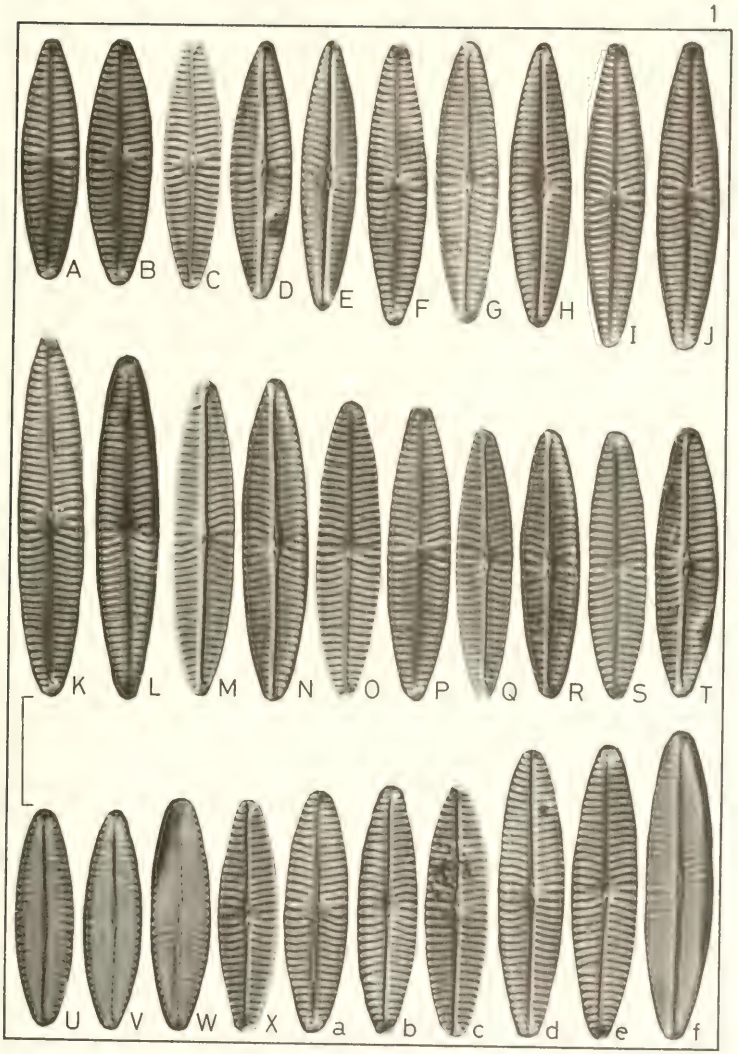
Plate 2, Figures A–c
FIGURES A–c. *Navicula recens* (× 2000). FIGURES A–J. Valves with slightly acute apices (89.2 %). FIGURES K–T. Valves with small size of central area (16.6 %). FIGURES U–c. Valves with standard size of central area (83.4 %).

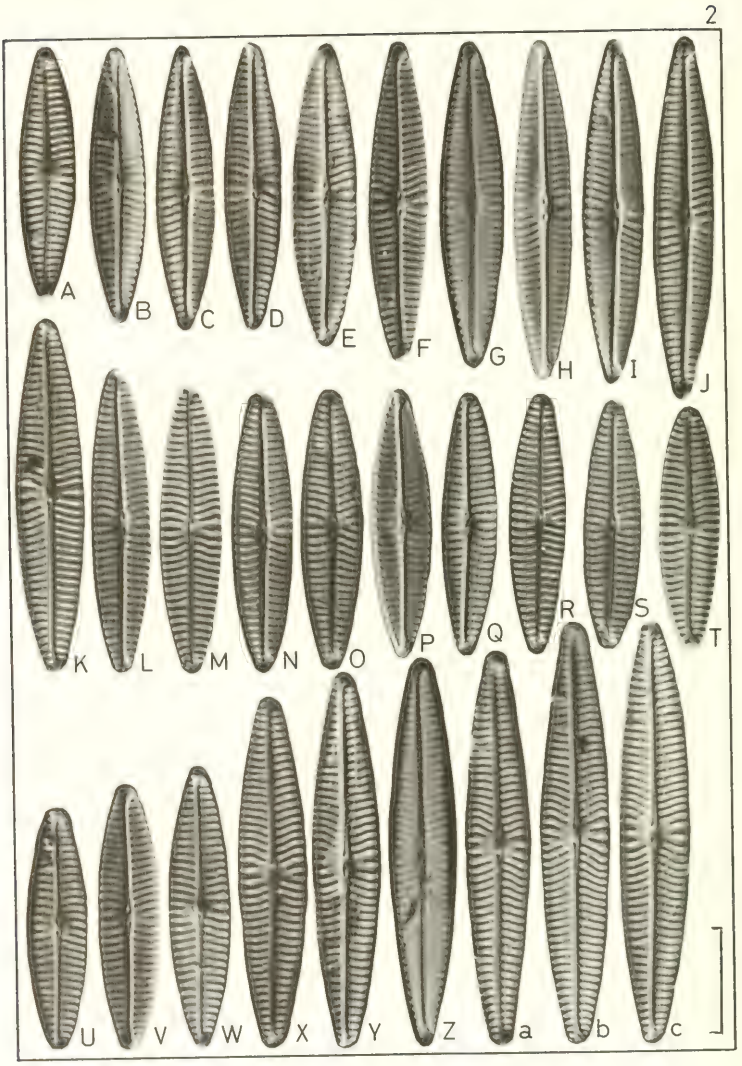
Plate 3, Figures A–c
FIGURES A–c. *Navicula recens* (× 2000). FIGURES A–I. Valves with larger central area at distaff side (14.8 %). FIGURES J–S. Valves with larger central area at staff side (16.1 %). FIGURES T–c. Valves with central area of similar size at staff and distaff sides (69.1 %).

Plate 4, Figures A–c
FIGURES A–c. *Navicula recens* (× 2000). FIGURES A–J. Valves with almost rounded central area (38.0 %). FIGURES K–T. Valves with almost square central area (8.6 %). FIGURES U–c. Valves with rectangular central area (5.4 %).

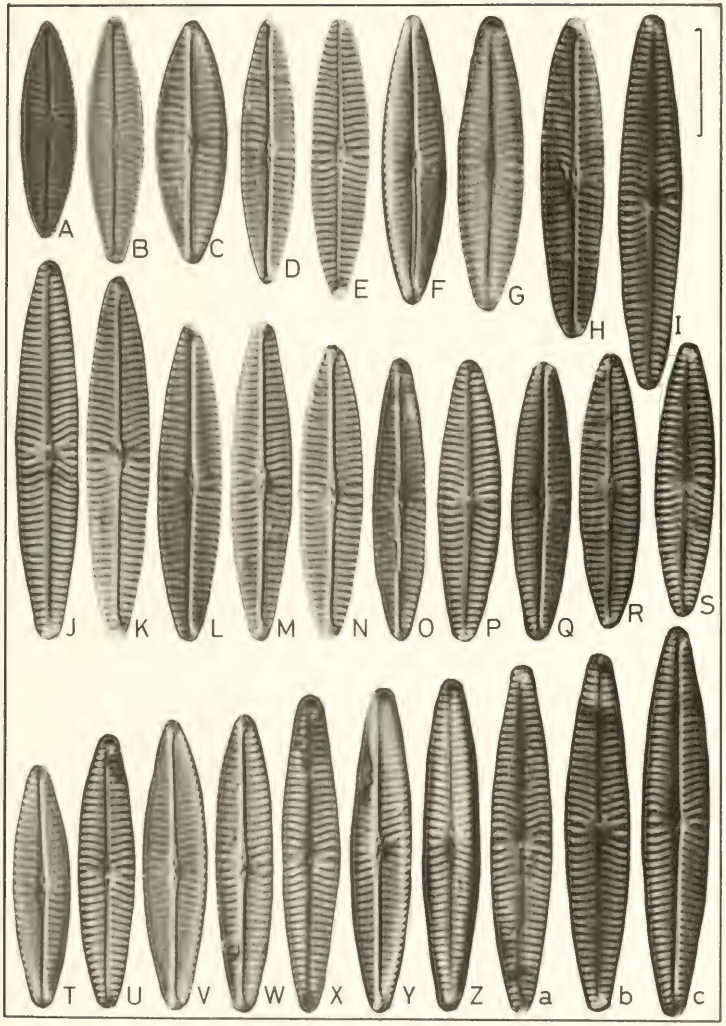
Plate 5, Figures A–c
FIGURES A–c. *Navicula recens* (× 2000). FIGURES A–J. Valves with almost rhombic central area (36.7 %). FIGURES K–T. Valves with different shape of the central area (11.3 %). FIGURES U–W. Valves with one Voigt fault at upper part of staff side (20.6 %). FIGURES X–d. Valves with one Voigt fault at lower part of staff side (7.2 %).

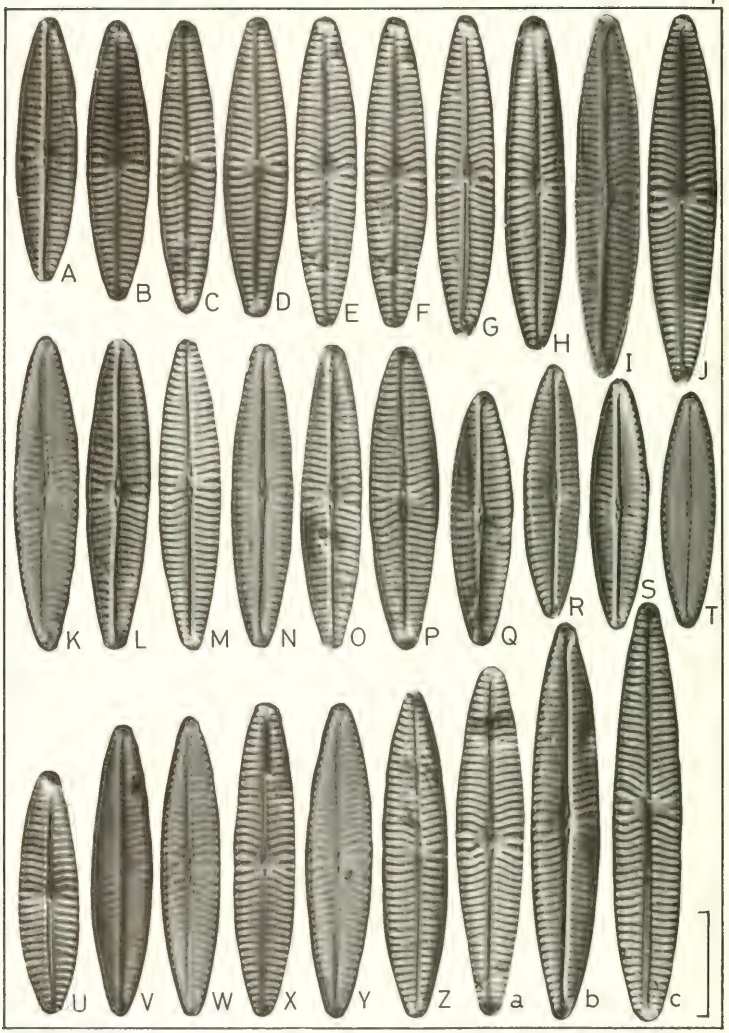
Plate 6, Figures A–e
FIGURES A–e. *Navicula recens* (× 2000). FIGURES A–D. Valves with two Voigt faults at the lower and upper parts of the staff side (8.5 %). FIGURES E–J. Valves without Voigt faults (61.1 %). FIGURES K–T. Valves with strongly radiate striae at the central part (17.9 %). FIGURES U–e. Valves with parallel or slightly parallel striae at central part (82.1 %).


1
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
a
b
c
d
e
f

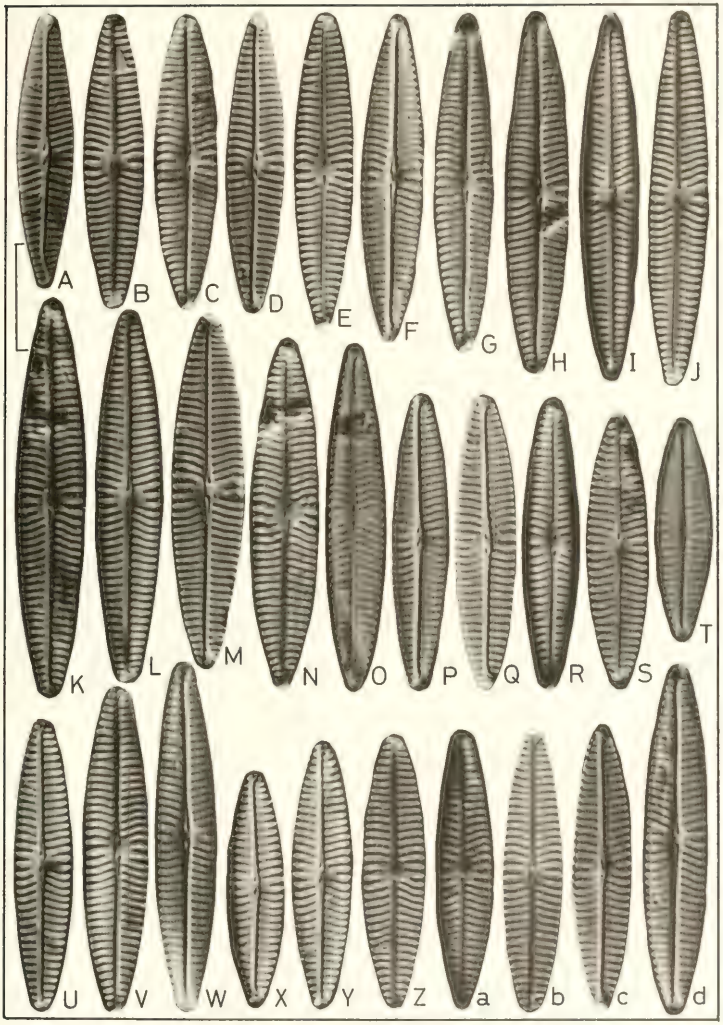

2
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
a
b
c

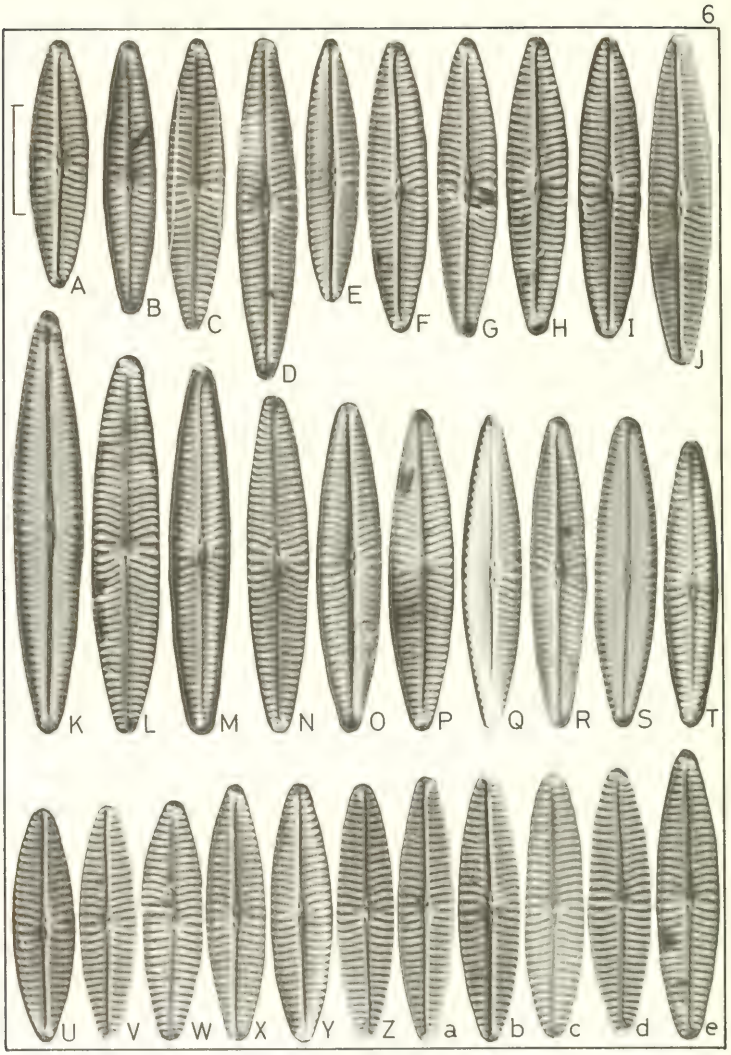
3




A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
a
b
c

5




6
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
a
b
c
d
e

The Freshwater Diatom Culture Collection At Loras College, Dubuque, Iowa

by

David B. Czarnecki

Department of Biology, Loras College, Dubuque, Iowa 52004-0178

with 1 table

Abstract: This report describes the status of the Loras College Freshwater Diatom Culture Collection as of 1 January, 1991. The Collection makes available more than 450 cultures, presently including 243 taxa from 57 genera and representing a numerical increase of nearly 90 % for strains and 50 % for taxa since the Collection was formalized in 1987. Ten taxonomic combinations, necessitated by current holdings, are included. Cultures are listed in alphabetical order along with their date of isolation and source. Explanations of culture protocol and access to the Collection are also provided.

Introduction

Until such time as successful cryopreservation (or similar) techniques are established for the maintenance of viable freshwater diatom cells (McLellan 1989), it appears that constant efforts must be directed at obtaining and maintaining culture isolates. One such effort, thus far restricted to North American strains, is reflected in the Freshwater Diatom Culture Collection at Loras College (Czarnecki 1987), a facility associated with the more inclusive Loras College Freshwater Algal Culture Collection (Czarnecki 1988, Czarnecki and Ross 1988). The goals of the Diatom Collection are aimed at increasing the diversity of maintainable, morphologically and physiologically healthy, unialgal and clonal freshwater diatoms that inherently are important for various and sundry investigations of biological significance.

Culture Protocol and Access

Cultures are maintained in tyndallized or, where appropriate, autoclaved biphasic CR1 or related medium (Czarnecki 1987, Czarnecki and Ross 1988), contained in 16 x 100 mm borosilicate glass tubes. These are subjected to an illumination combination of Cool White and Gro-lux fluorescent bulbs producing ca. 2500 lux, on a 14 hour light:10 hour dark time regime. Cultures are subjected to a temperature range of 17–23° C, dependent on ambient room conditions. Cultures are transferred into fresh media every 3–4 months.

Due to costs incurred, a fee schedule has been established, effective 1 July, 1990, that assesses each non-commercial user U. S. $15 ($25, commercial) per strain. Cultures will be sent in liquid phase, postage paid first class (air mail to foreign users) via U. S. Postal Service. Orders for cultures are accepted by letter or purchase order and should be directed

to the author, Department of Biology, Loras College, Dubuque, Iowa 52004-0178, or by telephone (319) 588-7231. Upon receipt of cultures, users will be sent an invoice reflecting the appropriate charges. Payments should be made in U. S. currency by check or bank draft and payable to Loras College Algal Culture Collection, account 117-925-132.

TABLE 1. Taxa (with **Codes**) no longer available from the Collection as reported by Czarnecki (1987).

Aulacoseira ambigua (Grun.) Simons., **03/03/A**
Caloneis sp. 1, **070**
Caloneis sp. 2, **A11**
Campylodiscus clypeus Ehrenberg, **50/01/A**
Cyclotella kuetzingiana Thwaites, **L70**
Cymbella proxima Reim.
Entomoneis alata (Ehrenberg) Ehrenberg, **003**
Entomoneis ornata (J. W. Bail.) Reim., **A72**
Gyrosigma obtusatum (Sulliv. & Wormley) Boyer, **017**
Hantzschia ?virgata (Roper) Grun., **039**
Mastogloia grevellei W. Sm., **L88**
Navicula capitata var. *hungarica* (Grun.) Ross, **L27**
Navicula peregrina (Ehrenberg) Kütz., **38/09/A**
Navicula viridula var. *linearis* Hust., **L43**
Neidium iridis var. *amphigomphus* (Ehrenberg) A. Mayer, **A49**
Pinnularia braunii var. *amphicephala* (A. Mayer) Hust., **A69**
Pinnularia ruttneri Hust., **A1**
Pinnularia viridis var. *intermedia* Cl., **A59**
Pinnularia viridis var. *minor* Cl., **A30**
Stauroneis anceps var. *americana* Reim., **029**
Stephanodiscus minutus Grun. *ex* Cl. & Möll., **A2**
Surirella sp. 1, **A8**

TAXONOMIC STATUS OF THE COLLECTION

Several strains (from 22 taxa) reported in Czarnecki (1987) are no longer viable and therefore have been dropped from the Collection. These are listed in Table 1.

In spite of these losses, the number of strains presently available exceeds 450 (see list of taxa currently maintained) and includes 243 ultimate taxa representing 57 genera, reflecting an increase in number of strains (ca. 90 %), ultimate taxa (ca. 50 %), and genera (ca 33 %). The increase in generic holdings is dependent on recent nomenclatural attitude (see Round et al. 1990) more so than on actual additions to the Collection. Much of this attitude reflects renewed recognition of characters of living cells as being taxonomically significant, e.g., nature of the plastid. Since the Collection is based on live cells, it is therefore more than appropriate to recognize the taxonomic value of this approach and follow the taxonomy presented in Round et al. (1990). However, this also necessitates taxonomic revision for certain strains, either maintained in the Collection, or their nominates. Nomenclatural revisions necessitated by these strains are offered below:

Achnanthidium affine (Grun.) comb. nov.
Basionym: *Achnanthes affinis* Grun. *in* Cl. & Grun., K. Svenska Vet.-Akad. Handl., Ny Följd, 17(2):20. 1880.

Achnanthidium exiguum (Grun.) comb. nov.
Basionym: *Stauroneis exilis* Kütz., Bacill., p. 105, Pl. 30, Fig. 21. 1844. [non *Achnanthes exilis* Kütz., 1833].

Synonym: *Achnanthes exigua* Grun. *in* Cl. & Grun., K. Svenska Vet.-Akad. Handl., Ny Följd, 17(2):21. 1880.

Achnanthidium exiguum var. ***heterovalvum*** (Krasske) comb. nov.
Basionym: *Achnanthes exigua* var. *heterovalva* Krasske, Bot. Arch., 3(4):193, Figs. 9a, 9b. 1923.

Achnanthidium minutissimum (Kütz.) comb. nov.
Basionym: *Achnanthes minutissima* Kütz., Linnaea, 8:578, Pl. 16, Fig. 54. 1833; Alg. Dec. 8, No. 75. 1833.

Craticula halophila f. ***robusta*** (Hust.) comb. nov.
Basionym: *Navicula halophila* f. *robusta* Hust., Österr. bot. Z., 106:401, Figs. 1–3. 1959.

Craticula halophila f. ***tenuirostris*** (Hust.) comb. nov.
Basionym: *Navicula halophila* f. *tenuirostris* Hust., Int. Rev. ges. Hydrobiol., 42(1):52, Fig. 76. 1942.

Encyonema minutum var. ***pseudogracilis*** (Choln.) comb. nov.
Basionym: *Cymbella turgida* var. *pseudogracilis* Choln., Portugaliae Acta., Ser. B, 6(2):112, Pl. 2, Figs. 49, 50. 1958.

Synonym: *Cymbella minuta* var. *pseudogracilis* (Choln.) Reim. *in* Patr. & Reim., Monogr. 13, Acad. Nat. Sci. Philadelphia, 2(1):50, Pl. 9, Figs. 1a–2b. 1975.

Encyonema muelleri f. ***venticosa*** (Temp. & Perag.) comb. nov.
Basionym: *Encyonema turgidum* var. *ventricosa* Temp. & Perag., Diat. Monde Entier, 1st ed., p. 254. 1895.

Synonym: *Cymbella muelleri* f. *ventricosa* (Temp. & Perag.) Reim. *in* Patr. & Reim., Monogr. 13, Acad. Nat. Sci. Philadelphia, 2(1):44, Pl. 7, Figs. 3a–4. 1975.

Fragilariforma virescens var. ***capitata*** (Østr.) comb. nov.
Basionym: *Fragilaria virescens* var. *capitata* Østr., Danske Diat., p. 193, Pl. 5, Fig. 125. 1910.

Sellaphora pupula var. ***rectangularis*** (Greg.) comb. nov.
Basionym: *Stauroneis rectangularis* Greg., Quart. Jour. Micr. Sci., 2:99, Pl. 4, Fig. 17. 1854.

Synonym: *Navicula pupula* var. *rectangularis* (Greg.) Grun. *in* Cl. & Grun., K. Svenska Vet.-Akad. Handl., Ny Följd, 17(2):45. 1880.

Acknowledgements

The author would like to especially thank Dean Blinn, Charlie Reimer, Rex Lowe, Gene Stoermer, and the late Gerry Prescott for their advice, encouragement, and enthusiasm since the inception of the Collection. Jim Kuwabara and Cecily Chang of the United States Geological Survey graciously provided many live collections from Lake Tahoe that resulted in several successful isolates; Hedy Kling graciously provided collections and isolates, especially from Yellowstone Lake, and continues to provide helpful suggestions on culture and isolation techniques for centric diatoms. Continued support for the Collection by Loras College is greatly appreciated. A portion of the expansion of the Collection was funded through a grant from the Iowa Science Foundation. Importantly, gratitude is extended to all users of the Collection for giving it the utility for which it was developed.

Literature Cited

CHOLNOKY, B. J. 1958. Beiträge zur Kenntnis der sudafrikanischen Diatomeenflora. II. Einige Gewässer im Waterberg-Gebiet, Transvaal. Portugal. Acta Biol. (B), 6:101–153.

CLEVE, P. T. AND A. GRUNOW. 1880. Beiträge zur Kenntniss der arctischen Diatomeen. K. Svenska Vetenskapsakad. Handl., 17:1–121.

CZARNECKI, D. B. 1987. The freshwater diatom culture collection at Loras College, Dubuque, Iowa. Not. Nat. 465:1–16.

———. 1988. The Loras College non-diatom freshwater algal culture collection. Crypt. Algol. 9:203–209.

CZARNECKI, D. B. AND M. J. ROSS. 1988. The Itasca State Park algal culture collection at Loras College. J. Minn. Acad. Sci. 53:27–32.

GREGORY, W. 1854. Notice of the new forms and varieties of known forms occurring in the diatomaceous earth of Mull; with remarks on the classification of the Diatomaceae. Quart. J. Microsc. Sci. 2:90–100.

HUSTEDT, F. 1952. Süsswasser Diatomeen des indomalayischen Archipels und der Hawaii-Inseln. Int. Rev. ges. Hydrobiol. Hydrogr. 42:1–252.

———. 1959. Die Diatomeenflora des Neusiedler Sees im österreischischen Burgenland. Österr. bot. Z. 106:390–430.

KRASSKE, G. 1923. Die Diatomeen des Casseler Beckens und seiner Randgebirge, nebst einigen wichtigen Funden aus Niederhessen. Bot. Arch. 3:185–209.

KÜTZING, F. T. 1833. Synopsis Diatomearum oder Versuch einer systematischen Zusammenstellung der Diatomeen. Linnaea, 8:529– 620.

———. 1833–1836. *Algarum algae dulcis Germanicarum.* Decades 1– 16. Exsiccatae editae.

———. 1844. *Die kieselschaligen Bacillarien oder Diatomeen.* Köhne, Nordhausen. 152 pp.

MCLELLAN, M. R. 1989. Cryopreservation of diatoms. Diatom Res. 4:301–318.

ØSTRUP, E. 1910. *Danske diatomeer.* Copenhagen. 323 pp.

PATRICK, R. AND C. W. REIMER. 1975. *The diatoms of the United States exclusive of Alaska and Hawaii.* Vol. 2, Pt. 1. Monogr. Acad. Nat. Sci. Phila., No. 13. 213 pp.

ROEMER, S. C. AND J. R. ROSOWSKI. 1980. Valve and band morphology of some freshwater diatoms. III, Pre- and post-auxospore frustules and the initial cell of *Melosira roeseana.* J. Phycol. 16:399–411.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. *The diatoms.* Cambridge University Press, New York. 747 pp.

TEMPÈRE, J. AND H. PERAGALLO. 1889–1895. *Diatomées du monde entier.* 1st. ed. HY-tribout, Paris. 304 pp.

Loras College Diatom Cultures

Loras College Diatom Cultures are listed alphabetically by genus. Taxa are followed by **culture code**, date of isolation, and source; unless otherwise noted, cultures developed from single cell or colony (= clonal) isolates, were isolated by the author, and are maintained in CR1 medium.

Achnanthes Bory.
coarctata (Bréb. *in* W. Sm.) Grun., **064**, 25 II 81, Logan Cave, Benton Co., AR.

inflata (Kütz.) Grun. **063**, 25 II 81, Logan Cave, Benton Co., AR.

Achnanthidium Kütz. (= *Achnanthes* in part).
affine (Grun.) comb. nov., **L174**, 2 VI 88, Wahweap Cr., Kane Co., UT (in CHEV medium); **L210**, 2VI 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

exiguum var. *heterovalvum* (Krasske) comb. nov., **041** (as *Achnanthes exigua* var. *heterovalva* Krasske; Czarnecki 1987), 24 VIII 80, Mississippi R., Bemidji, MN (non-clonal).

lanceolatum Bréb. *in* Kütz., **18/02/B** (as *Achnanthes lanceolata* Bréb. *ex* Kütz.; Czarnecki 1987), 1976, Peck's L., Yavapai Co., AZ (non-clonal); **L215**, 2 XII 88, Wapsipinicon R., Wapsipinicon St. Park, IA; **L224**, 28 I 89, Wapsipinicon R., Wapsipinicon St. Park, IA.

microcephalum Kütz., **L48** (as *Achnanthes microcephala* (Kütz.) Grun.; Czarnecki 1987), 3 VII 85, L. Itasca, Itasca St. Park, MN (isolated by Dave Ongaro).

minutissimum (Kütz.) comb. nov., (Note: strains **18/01/A** and **073** were previously named as *Achnanthes minutissima* Kütz. [Czarnecki 1987]) **18/01/A**, 1975, L. Havasu, Mohave Co., AZ (non-clonal); **073**, 28 III 81, L. Fayetteville, Washington Co., AR (non-clonal).

rostratum Ostr., **A32** (as *Achnanthes rostrata* Ostr.; Czarnecki 1987), 19 XI 81, Mississippi R., Bemidji MN (non-clonal); **L225**, 28 I 89, Wapsipinicon R., Wapsipinicon St. Park, IA.

Amphipleura Kütz.
pellucida (Kütz.) Kütz., **L116**, 10 VII 87, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L117**, 13 VIII 87, L. Itasca, Itasca St. Park, MN.

Amphora Ehrenberg *ex* Kütz.
coffeiformis (Ag.) Kütz., **26/01/A**, 1975, Cholla L., Navajo Co., AZ (non-clonal; in CHEV medium).

copulata (Kütz.) Schoeman & Archibald, **L182**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L282**, 4 VIII 89, Heart L., Clearwater Co., MN.

pediculus (Kütz.) Grun., *fide* Krammer, **L190**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L218**, 29 X 88, Cedar R. at Iowa TH 1, Linn Co., IA.

veneta Kütz., **26/02/A**, 1976, Ashurst L., Coconino Co., AZ (non-clonal).

Anomoeoneis Pfitz.
sphaerophora (Ehrenberg) Pfitz., **31/01/A**, 1975, Cholla L., Navajo Co., AZ (non-clonal; in CHEV medium); **L211**, 27 VII 88, L. Itasca, Itasca St. Park, MN.

Asterionella Hass.

formosa Hass., **L61**, 10 X 85, Mississippi R., Dubuque, IA (non- clonal); **L325**, 15 VI 90, L. Tahoe, Placer Co., CA; **L326**, 15 VI 90, L. Tahoe, Placer Co., CA; **L368**, 8 X 90, Yellowstone L., Yellowstone National Park, WY (material from Hedy Kling).

Aulacoseira Thwaites (= *Melosira* in part).

granulata (Ehrenberg) Simons. var. *granulata* f. *granulata*, **A18**, 2 X 81, borrow pit at U. S. 30, W. Ames, IA; **L115**, 3 VIII 87, L. Itasca, Itasca St. Park, MN; **L217**, 28 X 88, Cedar R. at Iowa TH 1, Linn Co., IA, **L348**, 24 VII 90, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

granulata var. *angustissima* (O. Müll.) Simons. f. *angustissima*, **A7**, 30 VI 81, Beaver L. Res., Benton Co., AR (non-clonal).

granulata var. *angustissima* f. *spiralis* (Hust.) Czar. & Reinke, **L59**, 23 V 85, Mississippi R. (mi 579), Dubuque Co., IA.

italica (Ehrenberg) Simons. var. *italica*, **L-323**, 15 VI 90, L. Tahoe, Placer Co., CA; **L324**, 15 VI 90, L. Tahoe, Placer Co., CA.

italica var. *tenuissima* (Grun.) Simons., **A5**, 30 VI 81, Beaver L. Res., Benton Co., AR (non-clonal).

Bacillaria Gmelin.

paxillifer (O. Müll.) Hendey, **L126**, 9 IX 87, Mississippi R., Dubuque, IA (in CR1+ medium); **L127**, 9 IX 87, Mississippi R., Dubuque, IA (in CR1+ medium); **L181**, 18 X 88, Mississippi R. (opposite Platte R. inflow), Dubuque Co., IA (in CR1+ medium).

Caloneis Cl.

amphisbaena (Bory) Cl., **32/04/A**, 1977, Chevelon Cr., Navajo Co., AZ (non-clonal; in CHEV medium).

bacillum (Grun.) Cl., **32/01/A**, 1976, Colorado R., Coconino Co., AZ (non-clonal).

clevei (Lagerst.) Cl., **A38**, 21 I 82, Silver L. Fen, Dickinson Co., IA.

latiuscula var. *reimeri* Czar. & Blinn, **L160**, 13 IV 88, Montezuma Well Natl. Monument, Yavapai Co., AZ (in CR1+ medium).

lewisii Patr., **32/02/A**, 1976, Creek, 3 mi E of U. S. 89, Williams, AZ (non-clonal); **L207**, 27 VII 88, L. Bronson, L. Bronson St. Park, MN, **L359**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

limosa (Kütz.) Patr., **084**, City Pond, Fayetteville, AR.

ventricosa var. *ventricosa* (Ehrenberg) Meist., **L332**, 22 VIII 90, L. Tahoe, Placer Co., CA.

ventricosa var. *minuta* (Grun.) Mills, **A6**, 27 VI 81, City Pond, Fayetteville, AR (non-clonal).

ventricosa var. *subundulata* (Grun.) Patr., **L380**, 27 XI 90, Alimagnet L., Apple Valley, MN.

ventricosa var. *truncatula* (Grun.) Meist., **L281**, 31 VII 89, Excelsior Fens, Dickinson Co., IA (in CR1+ medium).

Chaetoceros Ehrenberg
muelleri Lemm., **055**, ?1980, Chevelon Cr., Navajo Co., AZ (isolated by Dean Blinn; ?non-clonal; in CHEV medium).

Cocconeis Ehrenberg
placentula var. *lineata* (Ehrenberg) V. H., **A-83**, 28 X 82, West L. Okoboji, Dickinson Co., IA; **L237**, 20 V 89, West L. Okoboji, Dickinson Co., IA.

Craticula Grun. (= *Navicula* in part).
cuspidata (Kütz.) D. G. Mann, (Note: strains **38/01/F** through **L74** were previously named as *Navicula cuspidata* [Kütz] Kütz.; Czarnecki 1987) **38/01/F**, 1976, Montezuma Well Natl. Monument, Yavapai Co., AZ; **38/01/G**, 1976, Cholla L., Navajo Co., AZ (in CHEV medium); **38/01/H**, 1976, Peck's L., Yavapai Co., AZ; **035**, 29 XI 79, ditch along AR TH 16, Madison Co., AR; **066**, 3 II 81, L. Fayetteville, Washington Co., AR; **A15**, 2 X 81, borrow pit at U. S. 30, W. Ames, IA; **A27**, 13 IV 82, Mississippi R., Bemidji, MN; **A-65**, 7 VI 82, West L. Okoboji, Dickinson Co., IA; **L21**, 17 VI 85, ditch along IA TH 311, Marshall Co., IA; **L28**, 23 IV 85, pond at Southview Blvd. and 21st Ave. S., West St. Paul, MN; **L31**, 23 IV 85, pond at Southview Blvd. and 21st Ave. S., West St. Paul, MN; **L36**, 29 IV 85, White Pine Hollow Cr., Dubuque Co., IA; **L74**, 7 VII 86, N. Deming Pond, Itasca St. Park, MN; **L118**, 10 VIII 87, L. Itasca, Itasca St. Park, MN; **L135**, 13 III 88, Kuapa Pond drain-age, Honolulu, HI (in CHEV medium); **L162**, 13 IV 88, Montezuma Well Natl. Mon-ument, Yavapai Co., AZ (in CR1+ medium); **L186**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L187**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L199**, 14 VII 88, West Fork Des Moines R., Estherville, IA; **L283**, 4 VIII 89, Heart L., Clearwater Co., MN; **L298**, 5 VIII 89, Quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L328**, 3 VI 90, Mississippi R., Redwing, MN; **L329**, 10 VII 90, L. Itasca, Itasca St. Park, MN, **L339**, 23 VII 90, West L. Okoboji, Dickinson Co., IA, **L341**, 15 VII 90, N. Deming Pond, Itasca St. Park, MN (in CR1-S medium), **L357**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA; **L358**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

halophila f. *robusta* (Hust.) comb. nov., **L171**, 2 VI 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

halophila f. *tenuirostris* (Hust.) comb. nov., **A21** (as *Navicula halophila* f. *tenuirostris* Hust.; Czarnecki 1987), 16 X 81, Skunk R., Story Co., IA.

Cyclostephanos Round *in* Theriot, Håkansson, Kociolek, Round & Stoermer.

invisitatus (Hohn & Hellerm.) Theriot, Stoermer & Håkansson, **L310** [identified by Hedy Kling], 5 III 90, L. Tahoe, Placer Co., CA.

Cyclotella (Kütz.) Bréb.
gamma Sov., **A84**, 6 VII 83, L. Itasca, Itasca St. Park, MN; **L101**, 10 VIII 87, L. Itasca, Itasca St. Park, MN; **L122**, 10 VIII 87, L. Itasca, Itasca St. Park, MN.

meneghiniana Kütz., **01/01/B**, 1977, Chevelon Cr., Navajo Co., AZ (non-clonal; in CHEV medium); **A9**, 8 VII 81, Beaver L. Res., Benton Co., AR (non-clonal); **A77**, 20 V 82, Des Moines R. at Co. E35, Boone Co., IA; **L37**, 23 VI 85, LaSalle Cr., Itasca St. Park, MN; **L38**, 23 VI 85, LaSalle Cr., Itasca St. Park, MN; **L76**, 28 VI 86, LaSalle Cr., Itasca St. Park, MN; **L100**, 1 VIII 87, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L123**, 30 IX 87, Wapsipinicon R. at U. .S 20, Buchanon Co., IA; **L140**, 13 III 88, Kuapa Pond drainage, Honolulu, HI; **L141**, 13 III 88, Kuapa Pond drainage, Honolulu, HI; **L188**, 12 VII 88, Lazy Lagoon, West L.

Okoboji, Dickinson Co., IA; **L197**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L213**, 14 VII 88, West Fork Des Moines R., Estherville, IA; **L256**, 22 VI 89, Sucker Brook, Clearwater Co., MN; **L275**, 30 VII 89, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L286**, 18 XII 89, L. Tahoe, Placer Co., CA; **L289**, 13 XII 89, L. Tahoe, Placer Co., CA; **L308**, 9 II 90, L. Tahoe, Placer Co., CA.

pseudostelligera Hust., **A14**, 2 X 81, borrow pit at U. S. 30, W. Ames, IA.

Cylindrotheca Rabh.

gracilis (Bréb. *ex* Kütz.) Grun. *in* V. H., **L85**, 15 VIII 86, cow's hoof imprint adjacent to Dugout Cr., Excelsior Fens area, Dickinson Co., IA (non-clonal; in 1/3 CHEV medium); **L156**, 12 IV 88, Wahweap Cr., Kane Co., UT.

Cymatopleura W. Sm.

elliptica (Bréb.) W. Sm., **L201**, 14 VII 88, Little Miller's Bay, West L. Okoboji, Dickinson Co., IA.

librile (Ehrenberg) Pant., **L-6**, 4 XII 84, Mississippi R., Dubuque, IA; **L216**, 29 X 88, Cedar R. at IA TH 1, Linn Co., IA.

Cymbella Ag.

aspera (Ehrenberg) H. Perag., **L120**, 10 VIII 87, L. Itasca, Itasca St. Park, MN; **L272**, 5 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L284**, 5 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN.

cistula (Ehrenberg) Kirchn., **L192**, 13 VII 88, Spring Run Preserve, Dickinson Co., IA; **L234**, 20 V 89, West L. Okoboji, Dickinson Co., IA; **L253**, 26 VI 89, Pool at L. Alice Springs, Hubbard Co., MN.

cymbiformis var. *nonpunctata* Font., **L254**, 16 VI 89, springs, Bearpaw Point, L. Itasca, Itasca St. Park, MN.

lanceolata (Ag.) Ag., **L195**, 13 VII 88, Spring Run Preserve, Dickinson Co., IA.

lata Grun., **L346**, 23 VII 90, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

mexicana (Ehrenberg) Cl., **L288**, 18 XII 89, L. Tahoe, Placer Co., CA.

microcephala Grun., **A78**, 9 IV 82, Silver L. Fen, Dickinson Co., IA; **L202**, 14 VII 88, Little Miller's Bay, West L. Okoboji, Dickinson Co., IA; **L279**, 4 VIII 89, Heart L., Clearwater Co., MN.

naviculiformis Auersw. *ex* Heib., **L244**, 22 VI 89, Sucker Brook, Iron Springs Bog, Clearwater Co., MN.

norvegica Grun., **L261**, 31 VII 89, Excelsior Fens, Dickinson Co., IA.

pusilla Grun., **L170**, 2 VI 88, playa lake along U. S. 70 and 82, ca. 4 mi S of Alamogordo, Otero Co., NM (in CHEV medium); **L229**, 9 III 89, L. Manitoba at Delta, MB, CANADA (in 2/3 CHEV medium).

tumida (Bréb. *ex* Kütz.) V. H., **L185**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L381**, 28 XI 90, Yacht Basin, Mississippi R., Dubuque, IA; **L383**, 28 XI 90, Mississippi R. at 16th St., Dubuque, IA.

Denticula Kütz.

elegans Kütz., **A81**, 6 VIII 82, Silver L. Fen, Dickinson Co., IA (in CR1+ medium); **A82** (near f. *valida* Pedic.), 6 VIII 82, Silver L. Fen, Dickinson Co., IA (non-clonal; in CR1+ medium).

Diadesmis Kütz. (= *Navicula* in part).
confervacea Kütz., **38/04/B** (as *Navicula confervacea* (Kütz.) Grun.; Czarnecki 1987), 1976, Montezuma Well Natl. Monument, Yavapai Co., AZ (non-clonal).

Diatoma Bory
tenue var. *elongatum* Lyngb., **L9**, 15 III 85, Retention Basin, Dubuque, IA; **L13**, 20 III 85, Retention Basin, Dubuque, IA.

Diploneis Ehrenberg *ex* Cl.
elliptica (Kütz.) Cl., **L68**, 31 III 86, Bergen Swamp, Genesee Co., NY.

Encyonema Kütz. (= *Cymbella* in part).
lunatum (W. Sm. *in* Grev.) V. H., **L143**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

minutum (Hilse *in* Rabh.) D. G. Mann var. *minutum*, **023** (as *Cymbella minuta* Hilse *ex* Rabh.; Czarnecki 1987), 27 VI 79, Clear Cr., Washington Co., AR (non-clonal); **L297**, 5 VIII 89, Quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN.

minutum var. *pseudogracilis* (Choln.) comb. nov., **086** (as *Cymbella minuta* var. *pseudogracilis* (Choln.) Reim.; Czarnecki 1987), 17 V 81, L. Fayetteville, Fayetteville, AR; **L266**, 30 VI 89, Iron Springs Bog, Clearwater Co., MN; **L307**, 9 II 90, L. Tahoe, Placer Co., CA.

muelleri (Hust.) D. G. Mann, **L53** (as *Cymbella muelleri* Hust.; Czarnecki 1987), 21 VI 85, L. Itasca, Itasca St. Park, MN; **L294**, 20 XII 89, L. Tahoe, Placer Co., CA.

muelleri f. *ventricosa* comb. nov., **L236**, 20 V 89, West L. Okoboji, Dickinson Co., IA.

silesiacum (Bleish *ex* Rabh.) D. G. Mann, **L72** (as *Cymbella minuta* var. *silesiaca* (Bleish *ex* Rabh.) Reim.; Czarnecki 1987), 21 VI 86, N. Deming Pond, Itasca St. Park, MN.

triangulum (Ehrenberg) Kütz., **012** (as *Cymbella triangulum* (Ehrenberg) Cl.; Czarnecki 1987), 5 II 80, Spring Cr., Benton Co., AR (non-clonal); **L196**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L365**, 8 X 90, Peosta Channel, Mississippi R., Dubuque, IA.

Entomoneis Ehrenberg
paludosa (W. Sm.) Reim., **21/03/A**, 1975, Cholla L., Navajo Co., AZ (in CHEV medium); **L-65**, 6 XII 85, Site I, Rempe Mine Area, Mahaska Co., IA (isolated by Mary Pat Quaid; in CHEV medium); **L149**, 12 IV 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

Epithemia Kütz.

adnata var. *minor* (Perag. & Hérib.) Patr., **L238**, 20 V 89, West L. Okoboji, Dickinson Co., IA.

argus var. *longicornis* (Ehrenberg) Grun., **L260**, 31 VII 89, Excelsior Fens, Dickinson Co., IA.

turgida (Ehrenberg) Kütz., **L51**, 23 VI 85, LaSalle Cr., Itasca St. Park, MN; **L193**, 13 VII 88, Spring Run Preserve, Dickinson Co., IA; **L276**, 4 VIII 89, Heart L., Clearwater Co., MN; **L349**, 23 VII 90, Little Miller's Bay, West L. Okoboji, Dickinson Co., IA.

Eunotia Ehrenberg

arcus Ehrenberg, **L-71**, 31 III 86, Starr Rd. pond near G. W. Prescott residence, Genesee Co., NY.

curvata (Kütz.) Lagerst., **17/02/A**, 1975, Vail L., Coconino Co., AZ (non-clonal; many ?aberrant); **L56**, 2 VII 85, LaSalle Cr., Itasca St. Park, MN; **L111**, 5 VII 87, N. Deming Pond, Itasca St. Park, MN (isolated by Mark Edlund); **L144**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium); **L198**, 13 VII 88, Spring Run Preserve, Dickinson Co., IA.

flexulosa Bréb. *ex* Kütz., **L93**, 6 III 87, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

formica Ehrenberg, 17/01/A, **1975**, Mississippi R. at Co. 7, Beltrami Co., MN (many ?aberrant).

glacialis Meist., **L246**, 27 VI 89, Pond, South Park Drive, near Josephine L., Itasca St. Park, MN.

maior (W. Sm) Rabh., **L83**, 16 VII 86, Bog N of Co. 22, Beltrami Co., MN; **L242**, 21 VI 89, N. Deming Pond, Itasca St. Park, MN.

pectinalis (O. Müll.) Rabh. var. *pectinalis*, **17/03/A**, 1976, Montezuma Well Natl. Monument, Yavapai Co., AZ (non-clonal; many ?aberrant); **L145**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

pectinalis var. *minor* (Kütz.) Rabh., **L146**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium); **L203**, 28 VII 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

Fallacia Stickle & D. G. Mann (= *Navicula* in part).

pygmaea (Kütz.) Stickle & D. G. Mann, **A19** (as *Navicula pygmaea* Kütz.; Czarnecki 1987), 16 X 81, Skunk R., Story Co., IA; **A80** (as *Navicula pygmaea* Kütz.; Czarnecki 1987), 25 VIII 82, West L. Okoboji, Dickinson Co., IA; **L183**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

Fragilaria Lyngb.

capucina Desm. var. *capucina*, **L247**, 30 VI 89, Iron Spring Bog, Clearwater Co., MN (in CR1(S) medium).

capucina var. *mesolepta* Rabh., **L95**, 6 III 87, Mississippi R., Dubuque, IA.

crotonensis Kitton, **L18**, 20 III 85, Retention Basin, Dubuque, IA; **L44**, 23 V 85, Green L., Dubuque Co., IA; **L110**, 3 VIII 87, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L184**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA; **L299**, 21 VI 89, L. Itasca, Itasca St. Park, MN (isolated by Shelia Stewart); **L369**, 8 X 90, Yellowstone L., Yellowstone Natl. Park, WY (material from Hedy Kling).

vaucheriae (Kütz.) Peters., **L168**, 3 VI 88, Elk L., Itasca St. Park, MN.

Fragilariforma Williams & Round (= *Fragilaria* in part).

virescens var. *capitata* (Ostr.) comb. nov., **L165**, 3 VI 88, French Cr. drainage, Itasca St. Park, MN.

Frustulia Rabh.

vulgaris (Thwaites) DeT., **006**, 7 II 80, Spring Cr., Benton Co., AR (non-clonal); **A56**, 2 IV 82, Clear Cr. (Pammel Woods), Ames, IA.

Gomphonema Ehrenberg

acuminatum Ehrenberg var. *acuminatum*, **L194**, 13 VII 88, Spring Run Preserve, Dickinson Co., IA; **L243**, 27 VI 89, Pond, South Park Drive, near Josephine L., Itasca St. Park, MN.

acuminatum var. *clavus* (Bréb.) Grun., **022**, 26 XI 79, White R., Madison Co., AR (non-clonal); **L337**, 5 VII 90, Ice House Pond, UM Station, Itasca St. Park, MN.

acuminatum var. *pusilla* Grun., **A67**, 13 IV 82, bog N of Co. 22, Beltrami Co., MN.

affine Kütz. var. *affine*, **A31**, 19 IX 81, Mississippi R., Bemidji, MN; **L240**, 27 VI 89, pond, South Park Drive, near Josephine L., Itasca St. Park, MN.

affine var. *insigne* (Greg.) Andrews, **L41**, 23 V 85, Mississippi R. (9 mi island), Dubuque Co., IA.

angustatum (Kütz.) Rabh. var. *angustatum*, **L78**, 1 VII 86, Elk L. fen, Itasca St. Park, MN (isolated by Mark Edlund); **L306**, 9 II 90, L. Tahoe, Placer Co., CA.

angustatum var. *citera* Hohn & Hellerm., **A61**, 21 V 82, Clear Cr. (Pammel Woods), Ames, IA.

angustatum var. *productum* Grun., **L309**, 9 II 90, L. Tahoe, Placer Co., CA.

apicatum Ehrenberg, **021**, 24 X 79, Butterfield Pond, Fayetteville, AR.

gracile Ehrenberg *emend.* V. H., **22/06/A**, 1975, Cholla L., Navajo Co., AZ (non-clonal; in CHEV medium); **A66**, 13 IV 82, bog N of Co. 22, Beltrami Co., MN; **L52**, 2 VII 81, LaSalle Cr., Itasca St. Park, MN.

grunowii Patr., **L112**, 22 VII 87, N. Deming Pond, Itasca St. Park, MN (isolated by Mark Edlund).

intricatum Kütz., **L304**, 21 II 90, L. Tahoe, Placer Co., CA.

parvulum (Kütz.) Kütz., **L130**, 27 IX 87, Iowa R. at Co. 18, Marshall Co., IA; **L228**, 28 III 89, Des Moines R. at Eldon, Wapello Co, IA.

sphaerophorum Ehrenberg, **A70**, 15 VI 82, West L. Okoboji, Dickinson Co., IA.

subclavatum (Grun.) Grun., **027**, 26 XI 79, White R., Madison Co., AR.; **A52**, 13 IV 82, Mississippi R., Bemidji, MN.

truncatum Ehrenberg var. *truncatum*, **L99**, 26 V 87, Spring Run Preserve, Dickinson Co., IA; **L316**, 15 XI 89, Mississippi R., Dubuque, IA.

truncatum var. *capitatum* (Ehrenberg) Patr., **L55**, 14 VIII 85, LaSalle Cr., Itasca St. Park, MN; **L280**, 4 VIII 89, Heart L., Clearwater Co., MN.

Gyrosigma Hass.

acuminatum (Kütz.) Rabh., **L15**, 21 III 85, Rupp Hollow Cr., Dubuque, IA.

scalproides (Rabh.) Cl., **018**, 5 II 80, Root School Cr., Fayetteville, AR (non-clonal).

spencerii (Quek.) Griff. & Henfr. var. *spencerii*, **L158**, 12 IV 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

spencerii var. *curvula* (Grun.) Reim., **L176**, 2 VI 88, Chevelon Potholes, Navajo Co., AZ (in CHEV medium); **L180**, 2 VI 88, Chevelon Springs, Navajo Co., AZ (in CHEV medium).

Hantzschia Grun.

amphioxys (Ehrenberg) Grun. var. *amphioxys*, **46/02/A**, 1975, Ashurst L., Coconino Co., AZ (non-clonal); **L167**, 3 VI 88, FDR Park, Dubuque Co., IA.

amphioxys var. *maior* Grun., **A4**, 28 VII 81, Prickly Pear Cr., Cascade Co., MT.

elongata (Hantzsch) Grun., **A41**, 11 II 82, Mississippi R., Bemidji, MN; **L274**, 5 VIII 89, Quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L331**, 22 VIII 90, L. Tahoe, Placer Co., CA.

Mastogloia Thwaites *ex* W. Sm.

elliptica var. *danseii* (Thwaites) Cl., **27/01/A**, 1976, Chevelon Cr., Navajo Co., AZ (in CHEV medium); **L87**, 16 VIII 86, Silver L. Fen, Dickinson Co., IA (in CHEV medium); **L231**, 17 III 89, L. Manitoba at Delta, MB, CANADA (in 2/3 CHEV medium).

smithii var. *lacustris* Grun., **L232**, 10 III 89, L. Manitoba at Delta, MB, CANADA (isolated by Ron Wheeler; in 2/3 CHEV medium).

Melosira Ag.

varians Ag., **L1**, 19 VI 84, LaSalle Cr., Itasca St. Park, MN; **L11**, 20 III 85, Retention Basin, Dubuque, IA; **L107**, 30 VI 87, Chambers Cr., Itasca St. Park, MN (isolated by Mark Edlund); **L290**, 13 XII 89, L. Tahoe, Placer Co., CA; **L367**, 8 X 90, Yellowstone L., Yellowstone Natl. Park, WY (material from Hedy Kling); **L379**, 26 XI 90, Mississippi R. at 16th St., Dubuque, IA.

Meridion Ag.

circulare Ag., **L305**, 21 III 90, L. Tahoe, Placer Co., CA.

Navicula Bory

agrestis Hust., **L366**, 8 X 90, Yellowstone L., Yellowstone Natl. Park, WY (material from Hedy Kling).

arvensis Hust., **38/02/A**, 1975, Peck's L., Yavapai Co., AZ (non-clonal).

capitoradiata (Kütz.) Compère, **L287**, 18 XII 89, L. Tahoe, Placer Co., CA; **L376**, 27 XI 90, Alimagnet L., Apple Valley, MN; **L377**, 27 XI 90, Alimagnet L., Apple Valley, MN; **L378**, 27 XI 90, Alimagnet L., Apple Valley, MN.

cari var. *cincta* (Ehrenberg) L.-Bert., **L230**, 9 III 89, L. Manitoba at Delta, MB, CANADA (in 2/3 CHEV medium); **L342**, 10 VII 90, L. Itasca, Itasca St. Park, MN.

cryptocephala Kütz. var. *cryptocephala*, **38/03/A**, 1975, Vail L., Coconino Co., AZ (non-clonal); **L263**, 3 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L278**, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L320**, 6 III 90, Mississippi R., Redwing, MN; **L356**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

cryptocephala var. *exilis* (Kütz.) Grun., **L344**, 6 VII 90, Elk L., Itasca St. Park, MN.

cryptocephala var. *veneta* (Kütz.) Rabh., **L154**, 12 IV 88, Chevelon Cr. Potholes, Navajo Co., AZ (in CHEV medium); **L335**, 22 VII 90, West L. Okoboji, Dickinson Co., IA.

decussis Østr., **L257**, 22 VI 89, Sucker Brook, Clearwater Co., MN; **L347**, 23 VII 90, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

heufleri var. *leptocephala* (Bréb. *ex* Grun.) Perag., **L172**, 2 VI 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

menisculus var. *upsaliensis* (Grun.) Grun., **L373**, 27 XI 90, Alimagnet L., Apple Valley, MN.

oblonga (Kütz.) Kütz., **L241**, 22 VI 89, L. Itasca, Itasca St. Park, MN.

pseudoexillisima Hust., **L291**, L. Tahoe, Placer Co., CA.

radiosa Kütz. var. *radiosa*, **L82**, 19 VII 86, N. Deming Pond, Itasca St. Park, MN; **L191**, 13 VII 88 Spring Run Preserve, Dickinson Co., IA; **L205**, 27 VII 88, L. Itasca, Itasca St. Park, MN; **L206**, 27 VII 88, L. Itasca, Itasca St. Park, MN; **L262**, 3 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L277**, 5 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L313**, 13 XII 89, L. Tahoe, Placer Co., CA.

radiosa var. *tenella* (Bréb. *ex* Kütz.) Grun., **L249**, 17 VI 89, Deming L., Itasca St. Park, MN.

reinhardtii var. *elliptica* Hérib., **L245**, 22 VI 89, Sucker Brook, Clearwater Co., MN.

rhynchocephala Kütz., **L136**, 13 III 88, Kuapa Pond drainage, Honolulu, HI.

seminuloides Hust., **L200**, 14 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

schroeteri Meist., **L315**, 29 XI 89, Mississippi R., Dubuque, IA.

tantula Hust., **L45**, 10 VII 85, L. Itasca, Itasca St. Park, MN (isolated by Rose Meier); **L327**, 19 V 90, Ice House Pond, UM station, Itasca St. Park, MN; **L340**, 5 VII 90, Ice House Pond, UM station, Itasca St. Park, MN.

tripunctata var. *schizonemoides* (V. H.) Patr., **L204**, 27 VII 88, L. Itasca, Itasca St. Park, MN.

trivialis L.-Bert., **38/07/A** (as *Navicula ?lanceolata* (Ag.) Kütz.; Czarnecki 1987), 1976, Creek, 3 mi E of U. S. 89, Williams, AZ (non-clonal); **L264**, 3 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN; **L292**, 20 XII 89, L. Tahoe, Placer Co., CA; **L375**, 27 XI 90, Alimagnet L., Apple Valley, MN.

viridula var. *rostellata* (Kütz.) Cl., **L353**, 10 VII 90, L. Itasca, Itasca St. Park, MN; **L363**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

vulpina Kütz., **L267**, 4 VIII 89, Heart L., Clearwater Co., MN.

Neidium Pfitz.

affine (Ehrenberg) Pfitz. var. *affine*, **L119**, 10 VIII 87, L. Itasca, Itasca St. Park, MN; **L265**, 13 VII 89, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium); **L322**, 21 V 90, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

affine var. *longiceps* (Greg.) Cl., **056**, 3 II 81, L. Fayetteville, Washington Co., AR; **L8**, 13 II 85, Retention Basin, Dubuque, IA; **L336**, 2 VII 90, Spencer's Pond, Itasca St. Park, MN.

affine var. *hankense* (Skv.) Reim., **L382**, 27 XI 90, Alimagnet L., Apple Valley, MN.

affine var. *tenuirostris* A. Mayer, **074**, 28 III 81, L. Fayetteville, Washington Co., AR; **L5**, 22 VI 84, Mississippi R., Bemidji, MN.

affine var. *undulatum* (Grun.) Cl., **L362**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

decens (Pant.) Stoermer, **028**, 7 II 80, Root School Cr., Fayetteville, AR; **L54**, 14 VIII 85, LaSalle Cr., Itasca St. Park, MN.

dubium (Ehrenberg) Cl., **A50**, 13 IV 82, Mississippi R., Bemidji MN (non-clonal).

iridis var. *subundulatum* (A. Cl.) Reim., **A28**, 14 I 82, Silver L. Fen, Dickinson Co., IA.

Nitzschia Hass.

acicularis W. Sm., **L10**, 12 III 85, retention basin, Dubuque, IA; **L12**, 20 III 85, retention basin, Dubuque, IA; **L248**, 22 VI 89, Sucker Brook, Iron Spring Bog, Clearwater Co., MN; **L302**, 21 II 90, L. Tahoe, Placer Co., CA; **L319**, 6 III 90, Mississippi R., Redwing, MN; **L360**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA; **L374**, 27 XI 90, Alimagnet L., Apple Valley, MN.

amphibioides Hust., **L79** (as *Nitzschia denticula* Grun.; Czarnecki, 1987), 16 VII 86, Bog n. of Co. 22, Beltrami Co., MN.

bryophila (Hust.) Hust., **L23**, 8 XII 84, retention basin, Dubuque, IA (isolated by Susan Walsh).

dissipata (Kütz.) Grun., **L285**, 18 XII 89, L. Tahoe, Placer Co., CA.

filiformis (W. Sm.) Schütt, **013**, 17 VI 80, 17 VI 80, Callion L., El Dorado Co., AR; **L129**, 19 X 87, Mississippi R., Dubuque, IA.

flexoides Geitler, **L300**, 22 VI 89, *Ophrydium versatile* colony, L. Itasca, Itasca St. Park, MN (isolated by Shelia Stewart); **L301**, 30 VII 89, *Ophrydium versatile* colony, L. Itasca, Itasca St. Park, MN (isolated by Shelia Stewart).

fruticosa Hust., **L57**, 2 VII 85, LaSalle Cr., Itasca St. Park, MN.

gandersheimensis Krasske, **L293**, 20 XII 89, L. Tahoe, Placer Co., CA.

gracilis Hantzsch, **L317**, 29 XI 89, Mississippi R., Dubuque, IA.

linearis (Ag. *ex* W. Sm.) W. Sm., **A62**, 1 IV 82, L. Laverne, ISU campus, Ames, IA; **L14**, 21 III 85, 21 III 85, Rupp Hollow Cr., Dubuque, IA; **L40**, 29 IV 85, White Pine Hollow Cr., Dubuque Co., IA; **L139**, 13 III 88, Kuapa Pond drainage, Honolulu, HI; **L226**, 28 I 89, Wapsipinicon R., Wapsipinicon St. Park, IA.

longissima var. *reversa* Grun., **L66**, 10 XII 85, Site I, Rempe Mine Area, Mahaska Co., IA (isolated by Mary Pat Quaid; in CHEV medium).

obtusa W. Sm., **45/13/A**, 1977, Chevelon Cr., Navajo Co., AZ (in CHEV medium); **L152**, 12 IV 88, Chevelon Cr. Potholes, Navajo Co., AZ (in CHEV medium); **L178**, 2 VI 88, playa lake along U.S. 70 and 82, ca. 4 mi S of Alamogordo, Otero Co., NM (in CHEV medium).

palea (Kütz.) W. Sm., **L46**, 12 VII 85, LaSalle Cr., Itasca St. Park, MN (isolated by Rose Meier); **L219**, 2 XII 88, Wapsipinicon R., Wapsipinicon St. Park, IA.

paleacea Grun., **45/12/A**, 1977, Chevelon Cr., Navajo Co., AZ (non-clonal; in CHEV medium); **L22**, 17 IV 85, ditch along IA TH 311, Marshall Co., IA.

recta Hantzsch, **A17**, 2 X 81, borrow pit at U. S. 30, W. Ames, IA.

romana Grun., **L208**, 27 VII 88, L. Itasca, Itasca St. Park, MN.

rostellata Hust., **L24**, 8 XII 84, Mississippi R., Dubuque, IA (isolated by Susan Walsh).

sigma (Kütz.) W. Sm., **A22** (s. lato, cf. var. *rigida* (Kütz.) Grun.), 16 X 81, Skunk R., Story City, IA; **L7** (s. lato, cf. var. *rigida* (Kütz.) Grun., 14 II 85, Retention Basin, Dubuque, IA; **L151**, 12 IV 88, Chevelon Cr. Potholes, Navajo Co., AZ (in CHEV medium).

sinuata var. *tabellaria* Grun., **049**, 3 II 81, L. Fayetteville, Washington Co., AR.

stagnorum Rabh., **L35**, 29 IV 85, White Pine Hollow Cr., Dubuque Co., IA.

vermicularis (Kütz.) Grun., **007** (inadvertently listed as *Stenopterobia intermedia* (Lewis) V. H.; Czarnecki 1987), 3 III 80, L. Fayetteville, Washington Co., AR.

vitrea Norman, **L177**, 2 VI 88, Chevelon Cr. Potholes, Navajo Co., AZ (in CHEV medium).

sp. 1 (cf. *frustulum* (Kütz.) Grun.), **45/01/A**, 1975, *Salvinia* culture, Carolina Biologicals (non-clonal).

sp. 2 (cf. *subacicularis* Hust.), **045**, 23 XII 80, Cave Springs, Benton Co., AR.

sp. 3, **L138**, 13 III 88, Kuapa Pond drainage, Honolulu, HI.

Orthoseira Thwaites (= *Melosira* in part).
?*epidendron* (Grun.) Crawford, **L163** (as *Melosira roseana* Rabh. *sensu* Roemer & Rosowski 1980), 3 VI 88, FDR Park (on mossy outcrop), Dubuque Co., IA.

Pinnularia Ehrenberg
acrosphaeria W. Sm., **L269**, 27 VI 89, Darling Pond, Itasca St. Park, MN.

appendiculata (Ag.) Cl., **L173**, 2 VI 88, Wahweap Cr., Kane Co., UT (in CHEV medium); **L351**, 24 VII 90, Excelsior Fens, Dickinson Co., IA; **L352**, 12 VII 90, Darling Pond, Itasca St. Park, MN.

biceps Greg., **L223**, 28 I 89, Wapsipinicon R., Wapsipinicon St. Park, IA.

bogotensis var. *undulata* (M. Perag.) Boyer, **L161**, 13 IV 88, Montezuma Well Natl. Monument, Yavapai Co., AZ (in CR1+ medium).

borealis Ehrenberg, **A25**, 2 XII 81, borrow pit at U. S. 30, W. Ames, IA (non-clonal).

braunii (Grun.) Cl., **082**, 27 VI 81, city pond, Fayetteville, AR.

brebissoni (Kütz.) Rabh., **L333**, 24 VII 90, Excelsior Fens, Dickinson Co., IA; **L334**, 24 VII 90, Excelsior Fens, Dickinson Co., IA.

gibba Ehrenberg, **L259**, 31 VII 89, Excelsior Fens, Dickinson Co., IA.

leptosoma Grun., **L84**, 16 VII 86, bog N of Co. 22, Beltrami Co., MN.

maior (Kütz.) Rabh., **A60**, 1 IV 82, L. Laverne, ISU campus, Ames, IA.

mesolepta (Ehrenberg) W. Sm., **L321**, 6 VI 90, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

nodosa (Ehrenberg) W. Sm., **L30**, 23 IV 85, pond along Hunter's Way Road, Apple Valley, MN.

stauroptera var. *subparallela* Mayer, **L189**, 12 VII 88, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

stomatophora (Grun.) Cl., **L209**, 28 VII 88, N. Deming Pond, Itasca St. Park, MN.

subcapitata Greg., **L147**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

substomatophora Hust., **L33**, 24 IV 85, pond at Southview Blvd. and 21st Ave. S., West St. Paul, MN; **L273**, 5 VIII 89, Excelsior Fens, Dickinson Co., IA (in CR1+ medium); **L296**, 5 XII 89, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

termitina (Ehrenberg) Patr., **L148**, 16 III 88, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

viridis (Nitz.) Ehrenberg var. *viridis*, **L255**, 22 VI 89, Sucker Brook, Iron Spring Bog, Clearwater Co., MN; **L355**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

viridis var. *commutata* (Grun.) Cl., **L73**, 21 VI 86, N. Deming Pond, Itasca St. Park, MN; **L268**, 27 VI 89, Darling Pond, Itasca St. Park, MN (in CR1(S) medium).

sp. 1, **067**, 26 I 81, Cave Springs, Benton Co., AR (non-clonal).

sp. 2, **068**, 3 II 81, L. Fayetteville, Washington Co., AR.

Placoneis Meresch. (= *Navicula* in part).
elginensis (Greg.) Cox, **L169**, 3 VII 88, Elk L., Itasca St. Park, MN.

Plagiotropis Pfitz.
lepidoptera var. *proboscidea* (Cl.) Reim., **004**, 27 X 80, Chevelon Cr., Navajo Co., AZ (in CHEV medium).

Pleurosigma W. Sm.
delicatulum W. Sm., **L64**, 6 XII 85, Site I, Rempe Mine Area, Mahaska Co., IA (isolated by Mary Pat Quaid; in CHEV medium); **L67**, 8 I 86, Site I, Rempe Mine Area, Mahaska Co., IA (non-clonal; in CHEV medium); **L233**, 9 III 89, L. Manitoba at Delta, MB, CANADA (isolated by Ron Wheeler; in 2/3 CHEV medium).

Pleurosira (Meneghini) Trevisan.
laevis (Ehrenberg) Compère, **L58**, 30 VII 85, Little Menomenee R. (Tranell Farm), Jo Daviess Co., IL (in CR1+ medium).

Rhoicosphenia Grun.
curvata (Kütz.) Grun., **L318**, 12 III 90, Mississippi R., Redwing, MN.

Rhopalodia O. Müll.
gibba (Ehrenberg) O. Müll. var. *gibba*, **39/02/A**, 1976, Cholla L. Navajo Co., AZ (many ?aberrant; in CHEV medium); **L86**, 8 VII 86, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L103**, 7 VII 87, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L227**, 29 I 89, L. Manitoba at Delta, MB, CANADA.

gibba var. *ventricosa* (Kütz.) H. & M. Perag., **39/01/A**, 1976, Cholla L., Navajo Co., AZ (many ?aberrant; in CHEV medium).

gibberula O. Müll. var. *gibberula*, **L179**, 2VI 88, Chevelon Cr. Springs, Navajo Co., AZ (in CHEV medium).

gibberula var. *vanheurckii* O. Müll., **L175**, 2 VI 88, Chevelon Cr. Potholes, Navajo Co., AZ (in CHEV medium).

Scoliopleura Grun.
peisonis Grun., **30/01/A**, 1976, Chevelon Cr., Navajo Co., AZ (many ?aberrant; in CHEV medium); **L150**, 12 IV 88, Chevelon Cr. potholes, Navajo Co., AZ (in CHEV medium).

Sellaphora Meresch. (= *Navicula* in part).
americana (Ehrenberg) D. G. Mann, **L81** (as *Navicula americana* Ehrenberg; Czarnecki 1987), 16 VII 86, N. Deming Pond, Itasca St. Park, MN; **L212**, 28 VII 88, N. Deming Pond, Itasca St. Park, MN.

laevissima (Kütz.) D. G. Mann, **A79** (as *Navicula laevissima* Kütz.; Czarnecki 1987), 25 VIII 82, West L. Okoboji, Dickinson Co., IA.

pupula (Kütz.) Meresch. var. *pupula*, **L338**, 10 VII 90, L. Itasca, Itasca St. Park, MN.

pupula var. *rectangularis* (Greg.) comb. nov., **L121**, 10 VIII 87, L. Itasca, Itasca St. Park, MN.

Stauroneis Ehrenberg
acuta W. Sm., **044**, 23 XII 80, Mississippi R., Bemidji, MN; **L350**, 24 VII 90, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

anceps Ehrenberg f. *anceps*, **33/01/A**, 1974, Lindberg Springs, Coconino Co., AZ (non-clonal); **L343**, 12 VII 90, Darling Pond, Itasca St. Park, MN.

anceps f. *gracilis* Rabh., **33/03/A**, 1975, Mississippi R., Bemidji, MN (non-clonal); **L20**, 17 IV 85, ditch along IA TH 311, Marshall Co., IA; **L250**, 13 VII 89, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium); **L330**, 5 VII 90, Ice House Pond, UM station, Itasca St. Park, MN.

obtusa Lagerst., **065**, 23 II 81, Logan Cave, Benton Co., AR.

phoenicenteron (Nitz.) Ehrenberg f. *phoenicenteron*, **L29**, 23 IV 85, pond at Southview Blvd. and 21st Ave. S., West St. Paul, MN.

phoenicenteron f. *gracilis* (Ehrenberg) Hust., **A54**, 13 IV 82, Mississippi R., Bemidji, MN (non-clonal); **L77**, 7 VII 86, N. Deming Pond, Itasca St. Park, MN; **L251**, 13 VII 89, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium); **L354**, 9 VII 90, Heart L. Pond, Clearwater Co., MN.

Staurophora Meresch. (= *Stauroneis* in part).
?*wislouchii* (Poretz. & Anis.) D. G. Mann, **L155**, 12 IV 88, Wahweap Cr., Kane Co., UT (in CHEV medium).

Stenopterobia Bréb. *ex* V. H.
curvula (W. Sm.) Krammer, **037** (as *Stenopterobia intermedia* (Lewis) V. H.; Czarnecki 1987), X 78, bog N of Co. 22, Beltrami Co., MN; **L252**, 27 VI 89, Darling Pond, Itasca St. Park, MN (in CR1(S) medium).

rautenbachiae Choln., **L271**, 10 VII 89, N. Deming Pond, Itasca St. Park, MN (in CR1(S) medium).

Stephanodiscus Ehrenberg

alpinus Hust., **L364**, 12 X 90, Yacht Basin, Mississippi R., Dubuque, IA.

binderanus (Kütz.) Kreiger, **L19**, 15 III 85, retention basin, Dubuque, IA.

hantzschii Grun., **L220**, 29 X 88, Cedar R. at IA TH 1, Linn Co., IA; **L221**, 2 XII 88, Wapsipinicon R., Wapsipinicon St. Park, IA; **L371**, ?3 X 90, Red River, MB, CANADA (isolated by Hedy Kling).

niagarae Ehrenberg var. *niagarae*, **L132**, 18 IV 88, Mississippi R., Dubuque Yacht Basin, Dubuque, IA; **L133**, 18 IV 88, Mississippi R., Dubuque Yacht Basin, Dubuque, IA; **L303**, 21 II 90, L. Tahoe, Placer Co., CA.

niagarae var. *magnifica* Fricke, **L345**, 23 VII 90, Lazy Lagoon, West L. Okoboji, Dickinson Co., IA.

parvus Stoermer & Håkansson., L370, ?23 VIII 90, Yellowstone L., Yellowstone Natl. Park, WY (isolated by Hedy Kling).

tenuis Hust., **L311**, 6 III 90, Mississippi R., Redwing, MN; **L312**, 6 III 90, Mississippi R., Redwing, MN; **L314**, 29 XI 89, Mississippi R., Dubuque, IA.

yellowstonensis Ther. & Stoermer, **L372**, ?22 VIII 90, Yellowstone L., Yellowstone Natl. Park, WY (isolated by Hedy Kling) [restricted use].

Surirella Turp.

angustata Kütz., **A26**, 2 XII 81, borrow pit at U. S. 30, W. Ames, IA.

brightwellii W. Sm., **49/03/A**, 1975, Cholla L., Navajo Co., AZ (non-clonal; in CHEV medium).

linearis W. Sm., **L125**, 27 IX 87, Wapsipinicon R. at U. S. 20, Buchanon Co., IA.

ovata Kütz. var. *ovata*, **A55**, 2 IV 82, Clear Cr. (Pammel Woods), Ames, IA.

ovata var. *africana* Choln., **032**, 27 XI 79, Clear Cr., Washington Co., AR.

ovata var. *apiculata* W. Sm., **L295**, 20 XII 89, L. Tahoe, Placer Co., CA.

robusta var. *splendida* (Ehrenberg) V. H., **L222**, 2 XII 88, Wapsipinicon R., Wapsipinicon St. Park, IA.

striatula Turp., **L164**, 2 VI 88, Chevelon Cr. Springs, Navajo Co., AZ (in CHEV medium).

Synedra Ehrenberg

acus Kütz., **L16**, 20 III 85, retention basin, Dubuque, IA; **L102**, 22 VII 87, Chambers Cr., Itasca St. Park, MN (isolated by Mark Edlund); **L235**, 20 V 89, West L. Okoboji, Dickinson Co., IA.

binodis (Ehrenberg) Chang & Steinberg, **009** (as *Synedra parasitica* var. *subconstricta* (Grun.) Hust.; Czarnecki 1987), 7 II 80, Spring Cr., Benton Co., AR.

delicatissima var. *angustissima* Grun., **L17**, 15 III 85, retention basin, Dubuque, IA; **L49**, 21 VI 85, L. Itasca, Itasca St. Park, MN.

nana Meist., **L113**, 3 VIII 87, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L239**, 23 V 89, L. Tahoe, Placer Co., CA.

rumpens (Kütz.) Hust., **L166**, 3 VI 88, Elk L., Itasca St. Park, MN.

ulna (Nitz.) Ehrenberg var. *ulna*, **A76**, 20 V 82, Des Moines R. at Co. E36, Boone Co., IA; **L32**, 21 IV 85, pond at Southview Blvd. and 21st Ave. S., West St. Paul, MN; **L108**, 30 VI 87, Chambers Cr., Itasca St. Park, MN (isolated by Mark Edlund); **L258**, 3 VIII 89, quarry, Co. Rd. 3, 3 mi N of L. Alice, Hubbard Co., MN.

ulna var. *oxyrhynchus* f. *mediocontracta* Hust., **L361**, 15 X 90, Maquoketa R., sec 30, R2W, T86N, Jones Co., IA.

Tabellaria Ehrenberg *ex* Kütz.
flocculosa (Roth) Kütz., **L94**, 6 III 87, Mississippi R., Dubuque, IA; **L104**, 3 VII 87, L. Itasca, Itasca St. Park, MN (isolated by Mark Edlund); **L106**, 30 VI 87, Chambers Cr., Itasca St. Park, MN (isolated by Mark Edlund); **L114**, 29 VII 87, L. Itasca, Itasca St. Park, MN.

Thalassiosira Cl.
pseudonana (Hust.) Hasle & Heim., **01/02/A**, 1977, Chevelon Cr., Navajo Co., AZ (non-clonal; in CHEV medium).

weissflogii (Grun.) G. Fryxell & Hasle, **L131**, 13 III 88, Kuapa Pond Drainage, Honolulu, HI.

Tryblionella W. Sm. (= *Nitzschia* in part).
debilis Arnott, **45/05/A** (as *Nitzschia tryblionella* var. *debilis* (Arnott) A. Mayer; Czarnecki 1987), 1975, Sphagnum culture, Carolina Biologicals (non-clonal).

hantzschiana Grun., **L27** (as *Nitzschia tryblionella* Hantz. var. *tryblionella*; Czarnecki 1987), 8 XII 84, retention basin, Dubuque, IA (isolated by Susan Walsh).

hungarica (Grun.) D. G. Mann, **45/11/A** (as *Nitzschia hungarica* Grun.; Czarnecki 1987), 1976, Cholla L., Navajo Co., AZ (non- clonal; in CHEV medium); **L153**, 12 IV 88, Chevelon Cr. potholes, Navajo Co., AZ (in CHEV medium); **L157**, 12 IV 88, Chevelon Cr. potholes, Navajo Co., AZ (in CHEV medium); **L214**, 29 X 88, Cedar R. at IA TH 1, Linn Co., IA.

levidensis W. Sm., **A74** (as *Nitzschia levidensis* (W. Sm.) Grun.; Czarnecki 1987), 15 VI 82, West L. Okoboji, Dickinson Co., IA.

Diatoms from Hypersaline Inland Waters of Egypt

by

P. Compère

Jardin Botanique National de Belgique,
Domaine de Bouchout, B-1860 Meise, Belgium

with 1 figure, 1 table, and 4 plates

Abstract: More than 60 diatom taxa were observed in samples from northern Egyptian water bodies with salinity that varied between 40 and 260 ‰. Diatoms were nowhere dominant or abundant; they were fairly common only in the localities with a relatively lower salt content (40–50 ‰) and were very scarce to totally absent from the localities with a salinity higher than 100 ‰. The most commonly occurring diatoms belonged to the genera *Achnanthes*, *Campylostylus*, *Cocconeis*, *Entomoneis*, *Fragilaria*, *Gyrosigma*, *Licmophora*, *Mastogloia*, *Nitzschia*, *Pleurosigma*, and *Rhopalodia*; some of them are illustrated by LM and SEM micrographs. A new variety of *Licmophora*, *L. gracilis* var. *aegyptiaca*, is described.

Introduction

In 1989 P. Baert collected a few plankton samples from hypersaline water bodies of northern Egypt while studying the biology and ecology of the brine shrimp (*Artemia*), part of a joint project of the Suez Canal University at Port Said and the State University of Ghent (Belgium). These samples were sent to Meise for identification of the algae. Though diatoms were not the most abundant organisms (small green or yellow green coccoid algae and/or green flagellates were dominant), more than 60 different diatom taxa were recognized. Waters with salinities of 40–50 ‰ were richest in species.

Materials and Methods

A total of six samples were considered and are described below. The localities where samples were collected are indicated in Figure 1.

Sample 1. Wadi el Natrum, Malaha el Sulfat; salinity: more than 200 ‰; pH: 9–10; temperature 30° C; depth: 15–40 cm. The dominant alga in the plankton is the green flagellate *Dunaliella parva* Larche (Chlorophyceae, Volvocales), which is accompanied by other phytoflagellates and a few trichomes of the blue-green algae *Spirulina platensis* (Nordst.) Geitl. and *Oscillatoria* spp. (Cyanophyceae). Diatoms are very scarce.

Sample 2. Fayum, Qarum lake salina; salinity: 50 ‰; depth: less than 1 m. One of the ponds of the salt-works. The main constituent of the plankton is a small marine coccoid green alga, *Nannochloris coccoides* Naumann, very similar to the yellow green *Nan-*

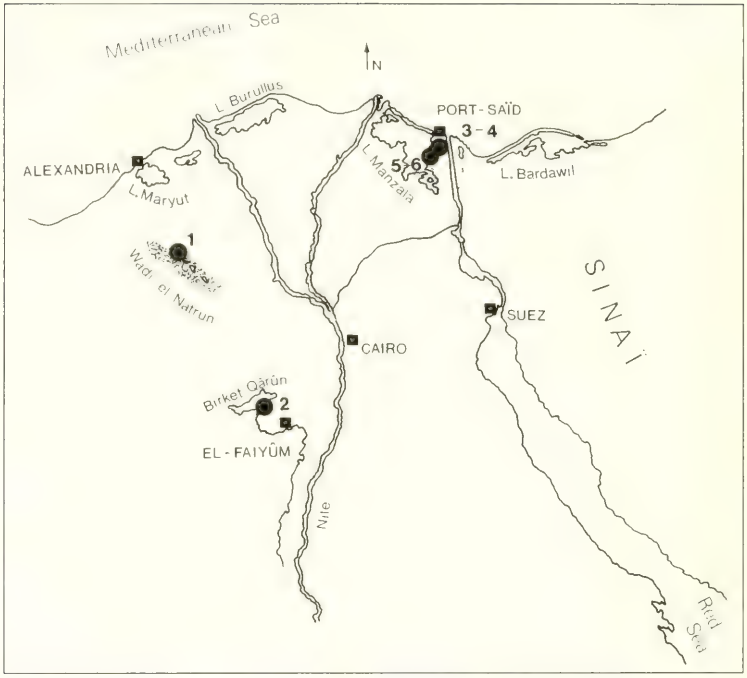


FIGURE 1. Map of lower Egypt with the sampling localities 1–6.

nochloropsis oculata (Droop) Hibberd from which it differs by the presence of chlorophyll b; among accompanying algae are *Prorocentrum micans* Ehrenberg, *P. minimum* Schiller (Dinophyceae) and some filaments of *Oscillatoria*. The diatoms are numerous and diverse; 37 taxa belonging to 18 genera were found.

Sample 3. Port Said, El Nasr Salina Company, evaporator 1; salinity: 100 ‰. Plankton dominated by *Nannochloris coccoides* with a few green flagellates of the genera *Dunaliella* and *Chlamydomonas* and a Cyanophyta-like organism matching "*Dactylococcopsis libyca*" Marchesoni. The diatoms are rare, mainly represented by *Nitzschia closterium*.

Sample 4. Port Said, El Nasr Salina Company, evaporator 3; salinity: 180 ‰. Phytoplankton scarce, with "*Dactylococcopsis libyca*" as the main component. Diatoms represented by a few valves of *Fragilaria*, *Licmophora*, and *Nitzschia*.

Sample 5. Port Said, Manzala Lake, Rassoua fish farm, intake canal; salinity: 40 ‰. Phytoplankton mainly comprised of *Nannochloris coccoides*, accompanied by a smaller, more cylindrical form resembling *Nannochloris bacillaris* Naumann, as well as "*Dactylococcopsis libyca*" and green flagellates of the genera *Chlamydomonas*, *Dunaliella*, and *Provasoliella*. The diatoms are somewhat more numerous and more diverse, with 26 taxa belonging to 15 genera encountered.

Sample 6. Port Said, Manzala Lake, Rassooua fish farm, pond °13; salinity: 260 ‰. Phytoplankton very poor, with a few *Dunaliella parva* and other flagellates. No diatoms, except for some unrecognizable fragments.

Results

The diatoms observed in the six samples are listed in Table 1, where the samples are arranged according to their salinity, and the relative abundance of the diatoms is indicated.

The total number of diatom taxa observed in these collections was 61, occurring mainly in the samples from water with relatively lower salinities (40–50 ‰). Water bodies with salinities higher than 100 ‰ were almost totally devoid of diatoms. In sample 2, 3, 4, and 5, the dominant alga was a very small marine green coccoid *Nannochloropsis coccoides*, characterized by the occurrence of chlorophyll b (pigment analysis, cf. P. Baert, in litt.); it was accompanied by some phytoflagellates, more numerous in samples 2 and 5 and by some Cyanophyta, including a peculiar organism, originally described by Marchesoni (1947:445) as "*Dactylococcopsis libyca*" (Chroococcales) but later considered by Drouet and Daily (1956:149) as "fungus spores." Indeed, specimens do resemble the artificial genus *Anguillospora* in the Hyphomycetes. In the highly hypersaline samples 1 and 6, the algae were less numerous and less diverse, mainly represented by the green flagellate *Dunaliella parva*. The diatoms were most numerous in sample 2, both in number of taxa and in number of individuals; in this sample, the most common diatoms were *Campylostylus normanianus*, *Fragilaria fasciculata*, *F.* cf. *tenera*, *Licmophora gracilis* var. *aegyptiaca*, *Mastogloia aquilegiae*, *Nitzschia closterium*, and *N. sigmaformis*. Diatom taxa were also fairly numerous in sample 5 (26) but in this case, each taxon was represented only by a few individuals. Two taxa, *Entomoneis alata* and *Gyrosigma balticum* var. *diminutum* were "fairly rare" (Table 1) in sample 5. There were still a few diatoms in sample 3, where *Nitzschia closterium* was fairly common and accompanied by other *Nitzschia* species, but diatoms were almost totally absent from samples 1, 4, and 6.

Taxonomic Notes

Amphora cymbelloides Grun. Small specimens, 25–35 µm long and 4.5–7 µm wide, with 20–25 striae in 10 µm; smaller than *A. angusta* Greg. and having finer striae, very much like *A. strigosa* Hust. from Sinai, which has coarser striae; marine. A few valves were found in samples 2, 3, and 5. Fig. 4.

Amphora aff. *montana* Krasske. One isolated valve, observed only in the SEM, 23.6 µm long and 4.8 µm wide, matching well in size and shape the micrographs of this freshwater species by Krammer and Lange-Bertalot (1986, Fig. 151:18–27) but with somewhat coarser striae (23 in 10 µm). Occurred in sample 3. Fig. 5.

Brachysira aponina Kütz. Small form, 18–20 × 4–4.2 µm, with about 40 striae in 10 µm. This taxon was reported from Bardawil lagoon (Egypt, N. Sinai) under the name *Navicula interruptistriata* Simonsen (Ehrlich 1975) and from Solar Lake (Israel) under the name *N. dvorachekii* Ehrlich (1978); both of these names are considered synonyms of *B. aponina* by Round and Mann (1981:227). Occurred in sample 2. Fig. 6.

Campylostylus normanianus (Grev.) Gerloff et al. Rather small form, with valves 88–175 × 9–12 µm. In the original description of *Synedra normaniana*, Greville (1862) cited two collections from Honduras, respectively by G. Shadbolt and by G. Norman. The latter is said to represent a small variety and the Shadbolt collection is the holotype of the species. Clearly, Shadbolt's gathering is represented in Greville diatom herbarium by the slide BM 2542 "Honduras, Smith, presented to me by Mr. Roper, May 1862," and not, as

TABLE 1. Diatoms observed in hypersaline waters of northern Egypt.

Number of sample	5	2	3	4	1	6
Salinity (‰)	40	50	100	180	200	260
Achnanthes brevipes var. *intermedia* (Kütz) Cl. (Figs. 2, 3)		+				
Amphora angusta Greg.	+		+			
A. coffeiformis (Ag.) Kütz.			+			
A. cymbelloides Grun. (Fig. 4)	+	+	+			
Aulacoseira granulata (Ehr.) Simonsen		+				
Brachysire aponina Kütz. (Fig. 6)		+				
Campylostylus normanianus (Grev.) Gerloff et al. (Figs. 7–13)		3	+			
Cocconeis diminuta Pant.	+	+				
C. placentula Ehr.		+				
Cyclostephanos dubius (Fricke) Round (Fig. 18)		1				
Cyclotella caspia Grun. (Fig. 14)		+				
C. glomerata Bachman (Figs. 15, 16)		+				
C. krammeri Håk	+	1				
C. meneghiniana Kütz.	+	+				
C. ocellata Pant.		1				
Cymbella pusilla Grun. ex A. Schm. (Fig. 17)	+					
Diploneis bombus (Ehr.) Cl.	+					
Entomoneis alata (Ehr.) Ehr. f. (Figs. 19, 20)	1					
E. paludosa (W. Sm.) Reimer f. (Figs. 21, 22)		1				
Eunotia curvata (Kütz.) Lagerst.		+				
Fragilaria capucina var. *vaucheriae* (Kütz) Lange-Bert.						+
F. fasciculata (Ag.) Lange-Bert.	+	2				
F. cf. *tenera* (W. Sm.) Lange-Bert. (Fig. 23)		3	+	+	+	
Gyrosigma acuminatum (Kütz.) Rabh. (Fig. 24)	+					
G. balticum (Ehr.) Rabh.	+					
G. balticum var. *diminutum* (Grun.) Card. et al. (Fig. 25)	1					
Hyalodiscus franklinii (Ehr.) R. Ross (Fig. 26)	+					
Licmphora gracilis (Ehr.) Grun. var. *aegyptiaca* Compère (Figs. 27–31)		2		+		
Mastogloia aquilegiae Grun. ex. A. Schm. (Figs. 32–34)		2				
M. braunii Grun.		+				
M. pumila (Grun.) Cl. (Figs. 35–37)	+	+				
M. punctifera Brun (Figs. 38, 39)	+					
M. pusilla Grun. (Figs. 40, 41)	+	+				
M. sirbonensis Ehrlich (Figs. 42, 43)		+				
Navicula bremeyeri Hust.		+				
N. duerrenbergiana Hust. (Fig. 44)		+				
N. ramosissima var. *torquata* (Harv.) Ross (Fig. 45)	+		+			
N. tenera Hust.	+					

TABLE 1, continued.

Number of sample	5	2	3	4	1	6
Salinity (‰)	40	50	100	180	200	260
Nitzschia closterium (Ehr.) W. Sm. (Fig. 47)	+		2		+	
N. circumscuta (Bail.) Grun.	+					
N. compressa (Bail.) Boyer var. *balatonis* (Grun.) Lange-Bert. (Fig. 46)	+					
N. constricta (Kütz.) Ralfs.	+					
N. fonticola Grun.	+					
N. hungarica Grun.		+				
N. liebentruthii Rabh.	+					
N. microcephala Grun.		1				
N. ovalis Arn. ex Grun.			+			
N. palea (Kütz.) W. Sm.		+	+			
N. pusilla Grun.		+				
N. cf. *scalpelliformis* (Grun.) Grun. (Figs. 49–51)		+	1	+		
N. sigma (Kütz.) W. Sm.			1			
N. sigmaformis Hust. (Fig. 48)		2				
N. stompsii Choln. (Fig. 52–54)		+				
Pleurosigma elongatum W. Sm. (Fig. 55)	+	1				
Rhopalodia musculus (Kütz.) O. Müll	1	1				
Stauroneis cf. *legleri* Hust. (Fig. 56)		+				
Stephanodiscus galileensis Håk. & Ehrlich (Fig. 57)		+				
Surirella striatula Turp. (Fig. 58)	+		1			
Surirella sp. (Figs. 59, 60)			+			
Number of taxa	27	37	14	3	3	-

stated by Williams (1988:49), by the slide BM 2543, which includes Norman's gathering as indicated on the label. Therefore, the holotype of *Synedra normaniana* Grev. is the slide BM 2542. In size and shape, the population from Qarum Lake matches the "small variety" of Greville (1862:232), as it is represented in Norman's material from Honduras, including even shorter specimens. The ultrastructure of this form examined in the SEM is identical with that depicted by Gerloff et al. (1978) for specimens from Jordan and by Wahrer et al. (1985) for American populations. The latter authors transferred the species into the genus *Licmophora*, because of similarities in morphology and ultrastructure with several species of this genus; however, their illustrations also show dissimilarities, namely in the structure of the areolae and striae (compare the striae of *L. normaniana*, Fig. 17, and those of *L. abbreviata*, Figs. 27, 28), and it could be wiser to keep both genera separated until *L. argentescens* Ag., the type species of *Licmophora*, has also been studied in the SEM. The species has been found in Bardawil lagoon, Egypt (Ehrlich 1975) and in saline water creeks in Jordan (Gerloff et al. 1978). Common in sample 2. Figs. 7–13.

Entomoneis alata (Ehrenberg) Ehrenberg Valve more than 100 µm long, with coarse striae, 11–12 in 10 µm, not composed of double rows of areolae as in *E. pulchra* (Bail.) Reimer. Also recorded from Bardawil lagoon (Ehrlich 1975). Not rare in sample 5. Figs. 19–20.

Entomoneis paludosa (W. Sm.) Reimer. Frustule 70–80 × 35–40 µm; striae 25–30 in 10 µm, finer than in var. *paludosa*, but somewhat coarser than in var. *duplex* (Donkin) Czarn. & Reinke. Junction line is smooth. Not rare in sample 2. Figs. 21–22.

Fragilaria aff. *tenera* (W. Sm.) Lange-Bertalot. Frustules 40–70 × 2–2.5 µm; 20–25 striae in 10 µm; the specimens collected by P. Baert match rather well W. Smith's original description including the "slightly inflated extremities" that do not appear on Hustedt's illustration (1931, p. 59: Fig. 703); they also match *Synedra nana* f. *capitata* Manguin from the Peruvian high mountains (Manguin 1964) and some densely striated forms included in *Synedra acus* by Germain (1981). All these, however, are freshwater species. Fairly abundant in sample 2; also found in samples 1, 3, and 4. Fig. 23.

Gyrosigma balticum (Ehrenberg) Rabenh. and var. *diminutum* (Grun.) Card. et al. The depicted specimen (Fig. 25) is 170 µm long, 17 µm wide and has 15–16 striae in 10 µm; it is more or less intermediate between *G. balticum* and *G. diminutum*. Shorter and longer specimens have been observed in this gathering; therefore the shorter specimens should not be classified in a different species but should be considered as a variety, as originally proposed by Grunow (1880) and recently confirmed by Cardinal et al. (1986:171). Fig. 25.

Licmophora gracilis var. **aegyptiaca** Compère, var. nov.

DESCRIPTIO: A var. gracile dimensionibus majoribus differt. Valvae 150–230 mm longae et 15–20 mm latae, clavatae, ad polum apicalem late rotundatae, ad basim longe attenuatae; area axialis conspicua, angusta, interiore prominens; striae punctatae, 22–26 in 10 mm; areolae secus aream axialem elongatae, in valva et ad margines breviores, subrotundatae; rimoportula plerumque 1 in valva, ad polum apicalem vel ad polum basalem, rariore 2, 1 in quoque polo. Fig. 27–31.

HOLOTYPUS: P. Baert n ° 2, lamina vitrea BR 1129 (BR).

COMMENTS: The population observed in sample 2 matches *L. gracilis* in shape and ornamentation but has frustules twice the size; no small specimens noted. Striae are also somewhat finer, and there are generally two labiate processes in a frustule: one at the apical pole of one valve and one at the basal pole of the other valve as in *L. onassis* Hust. (Simonsen 1987:372, Pl. 561, Figs. 10–16). This is different from the pattern observed by Wahrer et al. (1985:210) in *L. gracilis* var. *anglica* (Kütz.) Perag., where there are three labiate processes in each frustule, one at the headpole on both valves and one at the basal pole on only one valve. This pattern could be variable since Poulin et al. (1984: Figs. 34, 36) published SEM micrographs of valves of *L. gracilis* and *L. gracilis* var. *anglica* devoid of labiate processes at the head pole. Conversely, in the material from northern Egypt, some valves possess two labiate processes, one at each pole. *Licmophora gracilis* is a widespread marine species, also found in Bardawil lagoon. *Licmophora gracilis* var. *aegyptiaca* was observed in sample 2.

Mastogloia sirbonensis Ehrlich. Valves are 40–50 × 16–18 µm, with 18 striae in 10 µm; 3–4 median partecta are conspicuously larger than the others. Described from Bardawil lagoon, N. Sinai and distinguished from *M. braunii* mainly by the median partecta being abruptly larger than the others. A similar form had already been depicted by Schmidt (1893, Pl. 185, Fig. 45). Not always easy to distinguish from *M. braunii* since there are intermediate forms between those with partecta progressively enlarged from the pole to the median part and those with partecta becoming abruptly larger in the median part; also, the number of striae given for *M. sirbonensis* is included in the range given for *M. braunii* by Krammer and Lange-Bertalot (1986:433), and slightly protracted apices can be found in the latter; therefore, *M. sirbonensis* could be nothing more than a local variation of *M. braunii*. It was found in sample 2. Figs. 42, 43.

Navicula duerrenbergiana Hust. A rather small form, 28–30 × 4–4.5 µm with dense striae, to 18–20 in 10 µm. Rare in sample 2. Fig. 44.

Navicula ramosissima var. *torquata* (Harv.) R. Ross. [*N. mollis* (W. Sm.) Cleve]. Smaller valves, 20–25 × 4–5 µm with rounded apices. Rare, in samples 3 and 5. Fig. 45.

Nitzschia closterium (Ehrenberg) W. Sm. Weakly silicified valves, 80–100 × 3–3.5 µm, with about 20 fibulae in 10 µm. Not rare in samples 2 and 3, also found in sample 1. Fig. 47.

Nitzschia cf. *scalpelliformis* (Grun.) Grun. Valves 50–70 × 5–5.5 µm, with 10–11 fibulae and 25–30 striae in 10 µm. Smaller and more densely striated than *N. obtusa* W. Sm. Not very well differentiated from *N. vidovichii* Grun., which has a more central keel. Not rare in sample 4, a few valves also were encountered in samples 2 and 3. Figs. 49–51.

Nitzschia sigmaformis Hust. Long valves, 150–170 × 4–5 µm, very similar to *N. sigma*, but with a clear interruption of the fibulae in the middle; 10–11 fibulae and 30–32 striae in 10 µm. Not rare in sample 2. Fig. 48.

Nitzschia stompsii Choln. Valves 30–66 × 3–3.6 µm, with 11–14 fibulae and 26–32 striae in 10 µm; areolae arranged in longitudinal striae, as in *N. sigma* but the valves are not sigmoid. Occurred in sample 2. Figs. 52–54.

Pleurosigma elongatum W. Sm. Valves rather small and narrow, 160–180 × 18–20 µm, with 18–20 transverse and oblique striae in 10 µm. Difficult to separate from *P. delicatulum* W. Sm.: the rather coarse striae indicate *P. elongatum* but the narrow valve and the diagonal striae crossing each other at an angle somewhat less than 60 ° are characteristic of *P. delicatulum*. In marine and brackish water. Not rare in sample 2, a few specimens encountered in sample 5. Fig. 55.

Stauroneis cf. *legleri* Hust. Small and narrow form, with valves 31 × 5 µm and striae 18–20 in 10 µm in the middle to 24–28 in 10 µm near the poles. Included in *Navicula soodensis* Krasske by Kammer and Lange-Bertalot (1986:233). From inland saline waters of Austria. Rare in sample 2. Fig. 58.

Stephanodiscus cf. *galileensis* Håkansson & Ehrlich. A few valves were encountered, 25–30 µm diameter; radial fascicles of areolae uniseriate on the greater part of the valve surface; fascicles and spines 6–7 in 10 µm at the margin. Originally described from holocene sediments of lake Kinneret, Israel. Rare in sample 2. Fig. 57.

Surirella sp. Valves 50–60 × 27–32 µm, somewhat twisted in girdle view; surface costate-undulate with 30–45 costae in 100 µm. Occurs with *S. striatula* in sample 3. Figs. 59, 60.

Discussion and Conclusions

In the samples examined species diversity decreases sharply when salinity increases (Table 1); 27 and 36 diatom taxa were found respectively at salinities of 40 and 50 ‰, whereas 14 taxa were found at 100 ‰ salinity and 0–3 taxa, most probably represented only by dead frustules, at salinities higher than 180 ‰. This agrees with Noël's observations (1986:664) that most diatoms do not seem able to survive in salinities higher than 130 ‰.

A comparison with the flora of other hypersaline waters from Egypt (Ehrlich 1975), Israel (Ehrlich 1978), Libya (Ajaili et al. 1986), Spain (Noël 1986), France (Rince and Robert 1983, Noël 1986) show that more than 50 % of the taxa found in our samples have already been observed elsewhere in hypersaline waters. The majority of these diatoms belong to the holoeuryhaline group (Ehrlich 1975, Carpelan 1978a, b) since they are able to thrive in the whole range of salinities from fresh to hypersaline waters; a number are known to

tolerate more restricted ranges of salinities and could be described as marine eurytopic (10–100 ‰) or marine stenotopic (up to 40 ‰). Diatoms known only from freshwater are also present, but as the samples were formalin preserved, it is not possible to know whether they were actually living or only represented by dead frustules. Our samples share more than 20 taxa (35 %) with Lake Bardawil, on the Mediterranean shore of northern Sinai (Ehrlich 1975), including the rare species *Campylostylus normanianus* and *Mastogloia sirbonensis*. Of the 10 taxa observed in the highly hypersaline waters of Solar Lake, on the other side of the Sinai Peninsula (Ehrlich 1978), three are also in our samples: *Amphora coffeiformis*, *Brachysira aponina*, and *Navicula ramosissima* var. *torquata* (= *N. mollis*). Ajaili et al. (1986) observed 19 diatom taxa in an *Artemia* lake in Central Libya; only four of these, *Aulacoseira granulata*, *Cyclostephanos dubius*, *Cyclotella meneghiniana*, and *Nitzschia palea* are also in our samples. These four species are mainly known from freshwater but should probably be considered as holoeuryhaline since they can tolerate high salinities. Centric diatoms are scarce in our samples and totally absent from those with higher water salinities, which agrees with Noël's statement (1986:664) that "hypersaline waters are characterized by the lack or the scarcity of centric diatoms."

Acknowledgements

Thanks are due to Pat Sims (BM) for the loan of the original material of *Synedra normaniana*, to Hannelore Håkansson and Martha Ferrario for critical comments on some species, and to Marcel Verhaegen (BR) for help in handling the SEM and printing the micrographs.

Literature Cited

AJAILI, A., J. E. FURET, AND J. TANTI. 1986. Diatoms of a hypersaline lake in the Libyan Sahara. Pp. 645–653 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard (ed.). O. Koeltz, Koenigstein.

CARDINAL, A., M. POULIN, AND L. BÉRARD-THÉRIAULT. 1986. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. 5. Naviculales, Naviculaceae; les genres *Donkinia*, *Gyrosigma* et *Pleurosigma*. Naturaliste Can.113:167–190.

CARPELAN, L. H. 1978a. Revision of Kolbe's System der Halobien based on diatoms of California lagoons. Oikos 31:112–122.

———. 1978b. Evolutionary euryhalinity of diatoms in changing environment. Nova Hedwigia 29:489–526.

DROUET, F. AND W. A. DAILY. 1956. Revision of the coccoid Myxophyceae. Butler Univ. Bot. Stud. 12:1–218.

EHRLICH, A. 1975. The diatoms from the surface sediments of the Bardawil lagoon (Northern Sinai)—Paleoecological significance. Nova Hedwigia, Beih. 53:253–282.

———. 1978. The diatoms of the hypersaline Solar Lake (NE Sinai). Israel J. Bot. 27:1–13.

GERLOFF J., R. M. NATOUR, AND P. RIVERA. 1978. Diatoms from Jordan. Willdenowia 8:261–316.

GERMAIN, H. 1981. Flore des diatomées, eaux douces et saumâtres. Ed. Boubée, Paris. 444 p.

GREVILLE, R. K. 1862. Descriptions of new and rare diatoms. Serie VII. Quart. J. Miscrosc. Sci. n. s., 2:231–236.

GRUNOW, A. 1880. Bemerkungen zu den Diatomeen von Finmark, dem Karischen Meere und vom Jenissey nebst Vorarbeiten für Monographien der Gattungen *Nitzschia*, *Achnanthes*, *Pleurosigma*, *Amphiprora*, *Plagiotropis*, *Hyalodiscus*, *Podosira* und einiger *Navicula*-Gruppen. K. Sv. Vet. Akad. Handl. 17:16–121.

HUSTEDT, F. 1931–1959. Die Kieselalgen Deutschlands, Österreichs und der Schweiz Teil. 2. Pp. 1–845 *in* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, Band 7, L. Rabenhorst, ed. Akademische Verlagsgesellschaft, Leipzig.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae. 1. Teil: Naviculaceae. *In* Süsswasserflora von Mitteleuropa, Band 2, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. G. Fisher, Stuttgart. 876 p.

MANGUIN, E. 1964. Contribution à la connaissance des diatomées des Andes du Pérou. Mém. Mus. Nat. Hist. Nat., n. s., ser. B, Bot. 12:41–98.

MARCHESONI, V. 1947. Flora algologica del Fezzan e della regione di Gat. Mem. Ist. Ital. Idrobiol. Marchi 3:431–461.

NOEL, D. 1986. Les diatomées de deux marais salants méditerranéens:Salin-de-Giraud (S.E. de la France) et Santa Pola (Levant Espagnol). Similitudes et différences. Pp. 655–665 *in* Proceedings of the 8th Internatioal Diatom Symposium, M. Ricard, ed. O. Koeltz, Koenigstein.

POULIN, M., L. BÉRARD-THERRIAULT, AND A. CARDINAL. 1984. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. 2. Tabellarioideae et Diatomoideae (Fragilariales, Fragilariaceae). Naturaliste Can. 111:275–295.

RINCÉ, Y. AND J. M. ROBERT. 1983. Evolution des peuplements de diatomées planctoniques et benthiques d'un marais salant lors des variations printaniéres de salinité. Crypt. Algol. 4:73–87.

ROUND, F. E. AND D. G. MANN. 1981. The diatom genus *Brachysira* I. Typification and separation from *Anomoeoneis*. Arch. Protistenk. 124:221–231.

SIMONSEN, R. 1987. Atlas and catalogue of the diatom types of Friedrich Hustedt. 3 Vols. J. Cramer, Berlin.

WAHRER, R. J., G. A. FRYXELL, AND E. R. COX. 1985. Studies in pennate diatoms: valve morphologies of *Licmophora* and *Campylostylus*. J. Phycol. 21:206–217.

WILLIAMS, D. M. 1988. An illustrated catalogue of the type specimens in the Greville diatom herbarium. Bull. Brit. Mus. Nat. Hist. (Bot.) 18:1–148.

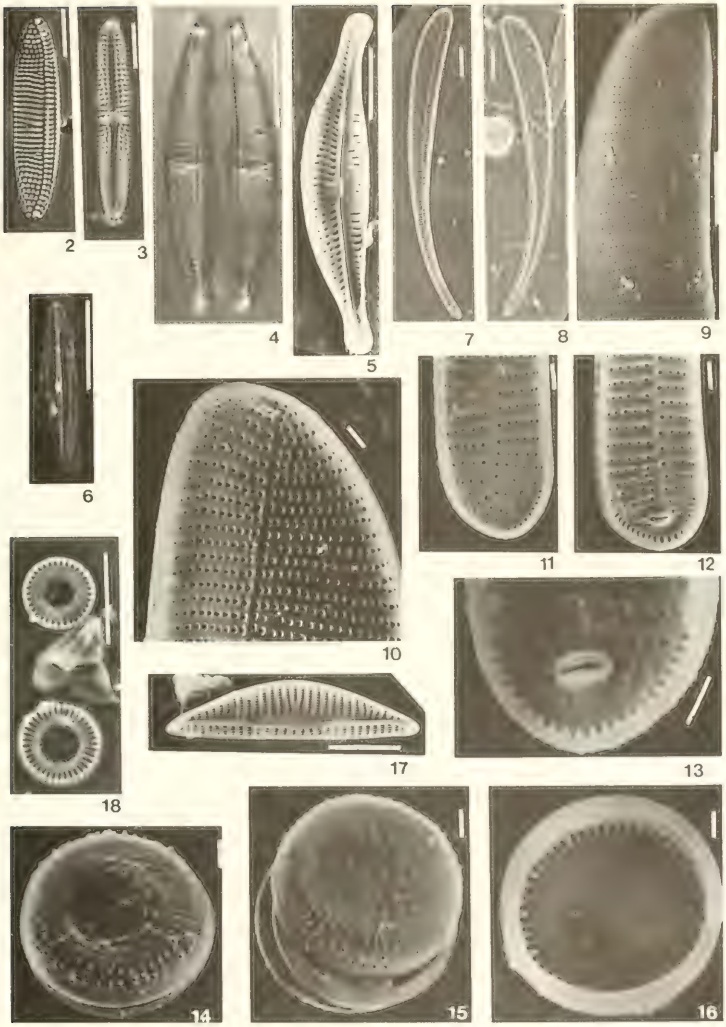
Explanation of Plates

Plate 1, Figures 2–18.
FIGURES 2, 3. *Achnanthes brevipes* var. *intermedia*. FIGURE 2. Rapheless valve, LM. FIGURE 3. Raphe valve, LM. FIGURE 4. *Amphora cymbelloides*, two valves, LM. FIGURE 5. *Amphora* aff. *montana*, valve interior, SEM. FIGURE 6. *Brachysira aponina*, LM. FIGURES 7–13. *Campylostylus normanianus*. FIGURES 7, 8. entire valves, LM. FIGURE 9. Headpole, external view, SEM. FIGURE 10. Headpole, internal view, showing labiate process, SEM. FIGURE. 11. Basal pole, internal view, without labiate process, SEM. FIGURE 12. Basal pole, internal view, with labiate process, SEM. FIGURE. 13. Labiate process at basal pole, SEM. FIGURE 14. *Cyclotella caspia*, frustule, exterior, SEM. FIGURE 15. *C. glomerata*, frustule, exterior, SEM. FIGURE 16. *C. glomerata*, valve interior, SEM. FIGURE 17. *Cymbella pusilla*, valve interior, SEM. FIGURE 18. *Cyclostephanos dubius*, 2 valves, LM. Scale bars = 10 µm for Figures 2–4, 6–8, 17, 18; 5 µm for Figures 5, 9; 1 µm for Figures 10–16.

Plate 2, Figures 19–31.
FIGURES 19, 20. *Entomoneis alata*. FIGURE 19. Valve view, LM. FIGURE 20. Detail of the striae, LM. FIGURES 21, 22. *E. paludosa*. FIGURE 21. Frustule in girdle view, LM. FIGURE 22. Valve exterior, SEM. FIGURE 23. *Fragilaria* aff. *tenera*, LM. FIGURE 24. *Gyrosigma acuminatum*, LM. FIGURE 25. *G. balticum* var. *diminutum*, LM. FIGURE 26. *Hyalodiscus franklinii*, convex valve, exterior, SEM. FIGURES 27–31. *Licmophora gracilis* var. *aegyptiaca*. FIGURE 27. Entire valve, LM. FIGURE 28. Headpole, LM. FIGURE 29. Inner septum, LM. FIGURE 30. Headpole, interior, with labiate process, SEM. Fig. 31. Basal pole, interior, with labiate process, SEM. Scale bars = 1 µm for Figure 31; 10 µm for all others.

Plate 3, Figures 32–51.
FIGURES 32–34. *Mastogloia aquilegiae*. FIGURE 32. Valve, LM. FIGURE 33. Valve exterior, SEM. FIGURE 34. Valve, interior showing partectal ring, SEM. FIGURES 35–37. *Mastogloia pumila*. FIGURE 35. Valve, focus on exterior, LM. FIGURE 36. Valve, focus on partecta. FIGURE 37. Internal view showing partectal ring, SEM. FIGURES 38, 39. *Mastogloia punctifera*, LM. FIGURE 38. Focus on valve exterior. FIGURE 39. Focus on partecta. FIGURES 40, 41. *Mastogloia pusilla*, LM. FIGURE 40. Focus on valve exterior. FIGURE 41. Focus on partecta. FIGURES 42, 43. *Mastogloia sirbonensis*, LM. FIGURE 42. Focus on valve exterior. FIGURE 43. Focus on partecta. FIGURE 44. *Navicula duerrenbergiana*, valve view, LM. FIGURE 45. *Navicula ramosissima* var. *torquata*, valve view, exterior, SEM. FIGURE 46. *Nitzschia compressa* var. *balatonis*, valve interior, SEM. FIGURE 47. *Nitzschia closterium*, frustule, LM. FIGURE 48. *Nitzschia sigmaformis*, frustule, LM. FIGURES 49–51. *Nitzschia* cf. *scalpelliformis*. FIGURE 49. Valve, LM. FIGURE 50. Valve interior, SEM. FIGURE 51. Valve interior showing detail of central nodule. Scale bars = 1 µm for Figures 46 and 51; 10 µm for all other figs.

Plate 4, Figures 52–60.
FIGURES 52–54. *Nitzschia stompsii*. FIGURE 52. Valve interior, SEM. FIGURE 53. Valve, LM. FIGURE 54. Valve, small form, LM. FIGURE 55. *Pleurosigma elongatum*, valve, LM. FIGURE 56. *Stauroneis* cf. *legleri*, valve, LM. FIGURE 57. *Stephanodiscus galileensis*, valve, LM. FIGURE 58. *Surirella striatella*, valve, LM. FIGURES 59, 60. *Surirella* sp., LM. FIGURE 59. valve view. FIGURE 60. Girdle view. Scale bars = 1 µm for Figure 52; 10 µm for all others.


2
3
4
5
7
8
9
6
10
11
12
18
17
13
14
15
16

19

20

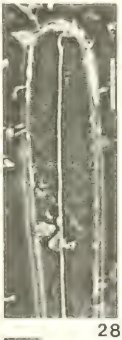
21

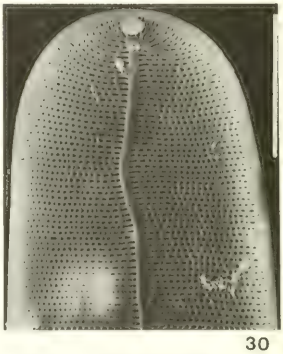
22

24

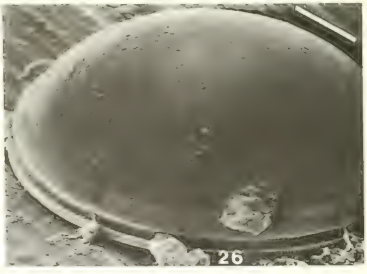
25

27


28

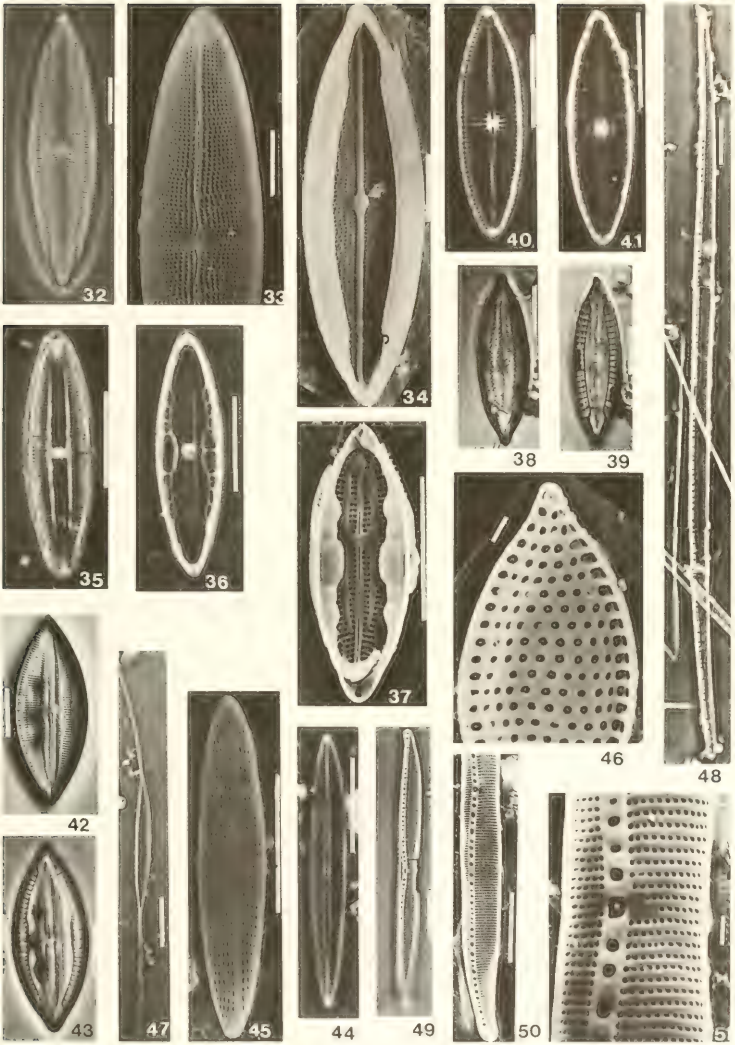

30

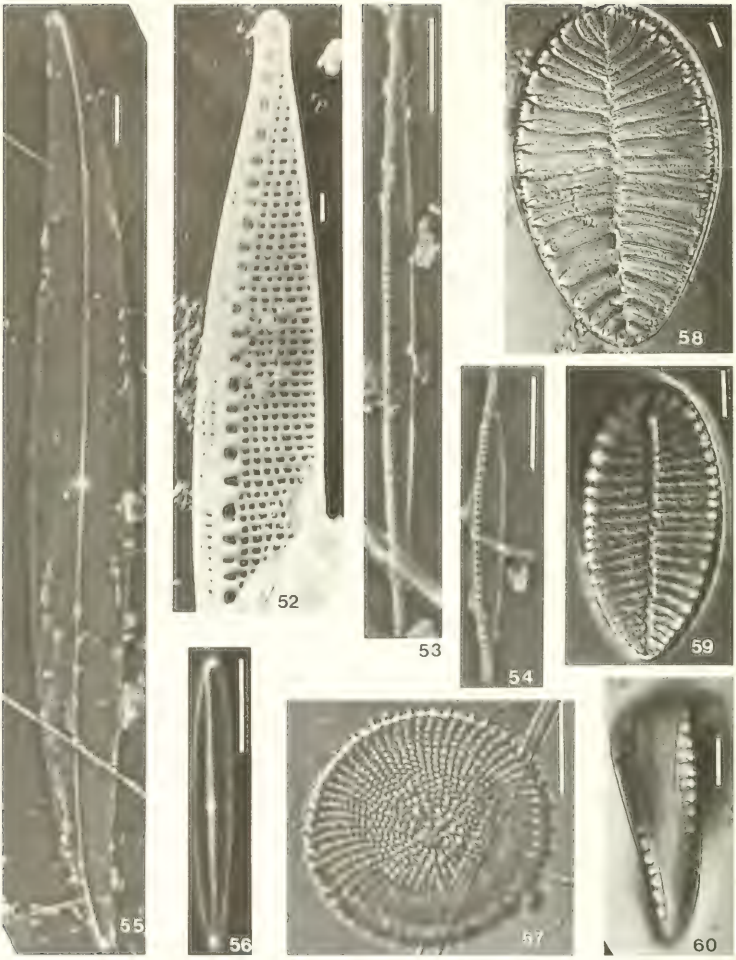
23


26

29

31


32
33
34
40
41
35
36
38
39
37
46
48
42
43
47
45
44
49
50


52
53
54
55
56
57
58
59
60

Mastogloia Species Associated With Active Stromatolites in Shark Bay, West Coast of Australia

by

Jacob John

School of Biology, Curtin University of Technology
GPO Box U 1987, Perth, W.A. 6001, Australia

with 1 figure and 5 plates

Abstract: Growing stromatolites are common in the hypersaline environment of Hamelin Pool in Shark Bay, Indian Ocean, west coast of Australia. Cyanobacteria and diatoms dominate the microbial communities in the algal mats associated with these stromatolites. *Mastogloia* was the most diverse diatom, represented by 36 species. The taxonomy and distribution of the *Mastogloia* species in the intertidal and subtidal microbial communities associated with the stromatolites, as well as the benthic communities of the basin, were investigated.

The fresh growing habit of several species of *Mastogloia* in the algal mat is characterized by mucilaginous tubes, strands, and capsules. The high diversity of *Mastogloia* species and their morphological variation are interpreted in terms of adaptations to the rigorous hypersaline environment experienced by the microbial communities. The probable role of *Mastogloia* species in stromatolite formation is discussed.

Introduction

The diatom *Mastogloia* is predominantly a tropical and subtropical genus of brackish, marine, and hypersaline waters, estimated to be represented by about 410 taxa (Hustedt 1959, and Novarino 1989). Species of *Mastogloia* are common in many shallow bays and hypersaline coastal lakes of Western Australia. This is not surprising considering the proximity of Western Australia to the Indo-Malaysian Islands, the center of the highest diversity of this genus (Hustedt 1959). One of the very early reports of *Mastogloia* (*M. macdonaldii* Grev.) was from Shark Bay (Wood 1963).

Shark Bay is well known for the largest array of living marine stromatolites in the world found in Hamelin Pool—a hypersaline lagoon of the bay (Figs. 1–3). Supratidal, intertidal, and subtidal stromatolite columns up to 1 meter are abundant in this region. The supratidal stromatolites are dead and are in varying stages of disintegration, whereas most of the subtidal stromatolites are covered by actively accreting algal mats. The intertidal stromatolites extend to high tide level and most have actively accreting living algal mats,

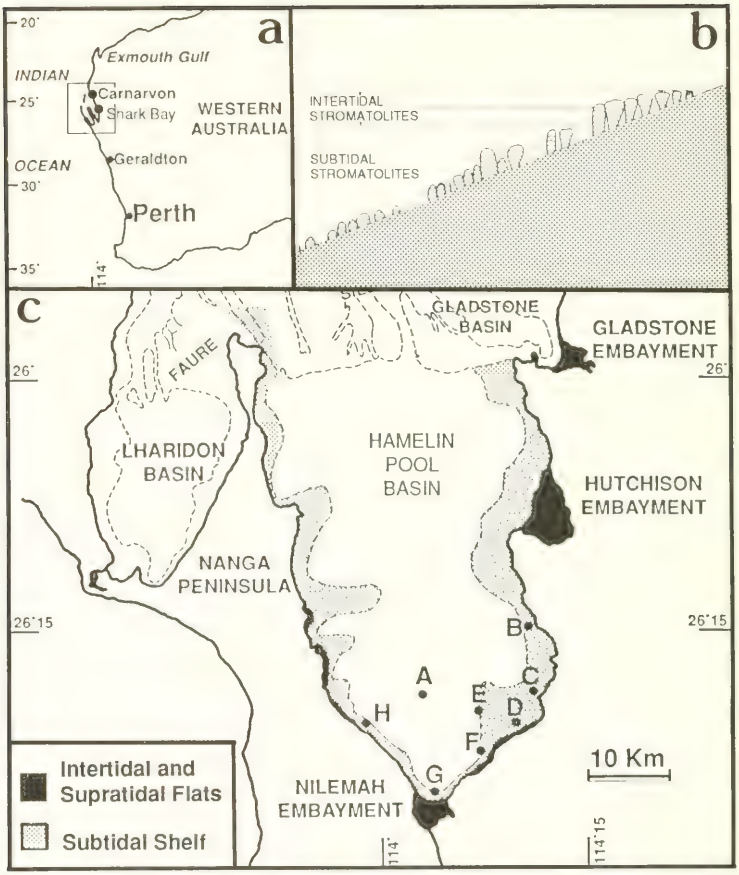


FIGURE 1. (a) Map of Western Australia showing the location of Shark Bay, (b) Diagrammatic section of Hamelin Pool illustrating the distribution of living algal stromatolites: subtidal stromatolites extend up to a depth of 3.5 m and the intertidal ones are shown between the high tide and low tide levels, (c) Hamelin Pool of Shark Bay with the sampling sites.

mainly on their sides (Figs. 1b, 2, 3). In some Hamelin Pool localities, supratidal, intertidal, and subtidal stromatolites form somewhat continuous patches.

All growing stromatolites are characterized by an envelope of soft sediment bound by algal mat (Playford and Cockbain 1976). These algal mats are composed of bacteria, cyanobacteria, green algae, and diatoms. Among the microbial communities, cyanobacteria have been widely considered as most important in stromatolite formation, and diatoms

have received very little attention (Hoffman 1976; Golubic 1976; Bauld 1984). In a continuing study of the microbial communities in Hamelin Pool, 80 diatom taxa have been recorded (John 1990), in contrast to probably fewer than 15 species of cyanobacteria and green algae. The highest diversity of diatoms was found in *Mastogloia*, represented by 36 species. The objective of this paper is to present the taxonomy and morphologic variation of these species with their general distribution pattern and their possible role in stromatolite formation.

Materials and Methods

Shark Bay is located between latitudes 24° 30' and 26° 45'S, 600 km north of Perth, the capital of Western Australia. Hamelin Pool in Shark Bay is a landlocked lagoon with restricted exchange with the ocean and partially separated from the rest of Bay by a shallow sea grass barrier bank—the Faure Sill (Fig. 1c). Evaporation in this arid region is very high (about 2200 mm per annum) and precipitation very low (about 210 mm per annum). These conditions result in the hypersaline environment of the lagoon with a salinity range of 55 ‰ in the north to 70 ‰ in the south throughout the year. Hamelin Pool consists of a broad central basin, 5–10 m deep, a sublittoral shelf less than 5 m deep, and a coastal strip in the intertidal and supratidal zone (Fig. 1c). Subtidal stromatolites are common up to several hundred meters offshore and up to a depth of 3.5 m in Hamelin Pool (Fig. 3).

Samples of algal mats from intertidal and subtidal stromatolites up to a depth of 3.5 m and top sediments from the central basin of Hamelin Pool from a depth of 4–7 m were hand collected in July 1983, November 1986, and January 1990. Salinity at sampling sites (Fig. 1c) ranged from 60–70 ‰. Fresh samples and cleaned diatom preparations were examined by a Vanox light photomicroscope and by scanning electron microscopy (JOEL JSM 35c) (John 1983). *Mastogloia* species were identified using specialized literature (Schimdt 1874–1959, Peragallo and Peragallo 1897–1908; Hustedt 1942, 1955, 1959; Voigt 1942, 1955; Hagelstein 1938; Hendey 1964; Patrick and Reimer 1966; Foged 1975, 1978, 1984; Ehrlich 1978; John 1980, 1983; Dexing et al. 1984; Simonsen 1987; Ricard 1987). Morphological variation and relative frequency of each species were also determined by light microscopy.

Results

A total of 36 species of *Mastogloia* were observed. The most relevant references, dimensions, and comments on morphology and distribution are given for the species in alphabetical order.

Mastogloia angulata Lewis
(Figs. 7–9)

REFERENCES: Hustedt (1959), p. 465, Fig. 885; Stephen and Gibson (1980) J. Phycol. 16, p. 355; John (1983), p. 116, Pl. 49, Fig. 1.

COMMENTS: Valve length 70–160 µm; width 30–40 µm, striae 9–10 in 10 µm, width of large middle partecta 3–4 µm; length 8–12 µm; width of small partecta 2.5–3.5 µm; length 3–4 µm. The valves are elliptical with slightly produced blunt apices and much larger than those reported by previous authors. The minimum length observed in the current population is within the maximum range reported by the above authors. The large middle partecta varied from one to three.

DISTRIBUTION: Specimens of the largest size range were found in the central basin of Hamelin Pool at a depth of 4–7 m and smaller specimens in both subtidal and intertidal algal mats.

Mastogloia asperula Grun.
(Figs. 10–12)

REFERENCE: Hustedt (1959), p. 480, Fig. 901.

COMMENTS: Length 50–80 µm; width 20–38 µm, striae 11–12 in 10 µm; areolae arranged in curved oblique lines 8 in 10 µm. Partecta uniform, reaching the apices, 4–5 in 10 µm and 2.5–3 µm wide with a slightly concave outer margin. Valves varied from broadly lanceolate to rhombic lanceolate with slightly produced apices.

DISTRIBUTION: Common in the basin, but not found in the intertidal mat and very rare in the subtidal mats.

Mastogloia aff. **asperuloides** Hust.
(Figs. 13–15)

REFERENCE: Hustedt (1959), p. 483, Fig. 902.

COMMENTS: Valve linear-lanceolate to rhombic-linear with raphe laterally expanded in the middle, 40–114 µm long, 20–40 µm wide. Striae arranged in transverse (12–13 in 10 µm) and areolae in oblique lines 7–8 in 10 µm. Central area wide. A single row of transapically elongated areolae is arranged closer to the axial area as shown by the SEM (Fig. 95). Partecta transapically rectangular, 3–3.5 µm wide and 2–2.5 µm long. This species differs from asperuloides in its shape being linear lanceolate or rhombic lanceolate and having less striae density. But the pattern of areolae in this taxon appears to be the same as in asperula and asperuloides.

DISTRIBUTION: Rare in subtidal algal mats and absent in intertidal mats, but common in the basin.

Mastogloia baldjikiana Grun.
(Figs. 16, 17)

REFERENCES: Hustedt (1959), p. 550, Fig. 981; John (1983) p. 117, Pl. 49, Figs. 3–6.

COMMENTS: Length 25–40 µm; width 10–15 µm, striae 19–22 in 10 µm, partecta 4–6 in 10 µm; 2.5 µm wide towards the middle and 1.5–2 µm towards the apices of the valve. The size range is considerably smaller than that reported in the Swan estuary, Perth, by John (1983).

DISTRIBUTION: Common in both intertidal and subtidal samples, but rare in the basin.

Mastogloia binotata (Grun.) Cl.
(Fig. 18)

REFERENCE: Hustedt (1959), p. 470, Fig. 889.

COMMENTS: Length 20–25 µm; width 13–17 µm, striae 15 in 10 µm, single partectum on each side of the valve occupying 1/3 of the length.

DISTRIBUTION: Rare, found only in the subtidal algal mats.

Mastogloia braunii Grun.
(Figs. 19, 20)

REFERENCES: Hustedt (1959), p. 551, fig. 982; Stephens and Gibson (1980), Nova Hedwigia 33:221–248; Patrick and Reimer (1966) p. 302, Pl. 20, figs. 18–19.

COMMENTS: Length 45–85 µm, width 13–20 µm; ratio of width to length 1:3–4, striae 16–18 in 10 µm, 3–5 partecta in the middle larger than the rest; the larger partecta 3–4 in 10 µm and the smaller ones 4–6 in 10 µm; width of the large partecta 2–3 µm and that of the small 1–2 µm. This species showed high variation in the number of large middle partecta and occasionally all partecta were found to be identical in size. The "H"-shaped hyaline area characteristic of the species (*sensu*, Hustedt, Patrick and Reimer) was traversed by faint areolae.

DISTRIBUTION: Common in all samples.

Mastogloia cocconeiformis Grun.
(Figs. 21, 22)

REFERENCE: Hustedt (1959), p. 469, Fig. 888.

COMMENTS: Length 34–100 µm; width 29–69 µm, striae 11–14 in 10 µm, partecta 6–7 in 10 µm; 4–5 µm wide. The size range of the population is higher than previously reported. Most of the valves are almost orbicular and the striae density is higher in smaller valves than in larger ones. The fresh growing habit of this species is characterized by long, gelatinous tubes composed of tiny strands emanating from the partecta. Individually each frustule is ensheathed by a gelatinous capsule as well (Figs. 5, 6). The mode of branching of these tubes is determined by the orientation of the cell division. A newly formed valve appears to secrete layers of mucilage around it as well as strands from the margin that coalesce to form the hollow tubes developing into an integrated meshwork along with the green alga cladophora and filamentous cyanobacteria.

DISTRIBUTION: Found abundantly in certain subtidal, rarely in some intertidal mats, and not in the basin.

Mastogloia corsicana Grun.
(Figs. 23, 24)

REFERENCE: Hustedt (1959), p. 533, Fig. 966.

COMMENTS: Length 28–31 µm; width 11–12 µm, striae 15–16 in 10 µm, partecta 7–8 in 10 µm; width 1.5–2.5 µm.

DISTRIBUTION: Very common in both subtidal and tidal algal mats, not observed in the basin.

Mastogloia cribrosa Grun.
(Fig. 25)

REFERENCES: Hustedt (1959), p. 468, Fig. 887; Stephens and Gibson (1979), Rev. Algol., 14, 1:21–32.

COMMENTS: Length 35–50 µm; width 25–35 µm, striae 9 in 10 µm, partecta 3 in 10 µm; width 3 µm. Fresh cells of this species were observed to have a gelatinous capsule and strands originating from the partectal ring.

DISTRIBUTION: Distributed in the subtidal mats, rare and not found in the basin.

Mastogloia crucicula (Grun.) Cl.
(Fig. 26)

REFERENCE: Hustedt (1959), p. 479, Fig. 894.

COMMENTS: Length 15–18 μm; width 7–8 μm, striae 20 in 10 μm, partecta 1–1.5 μm wide; 2 partecta on each side of the valve.

DISTRIBUTION: Rare, found in only very small numbers in the subtidal, intertidal, and basin samples.

Mastogloia decussata Grun.
(Figs. 27, 28)

REFERENCE: Hustedt (1959), p. 493, Fig. 917.

COMMENTS: Length 105–140 μm; width 30–41 μm, striae 28–30 in 10 μm, partecta 4 μm wide; 5–8 in 10 μm. The specimens in Hamelin Pool are larger than those reported by Hustedt.

DISTRIBUTION: Present in both subtidal mats and the basin but absent in intertidal mats.

Mastogloia aff. **elegans** Lewis
(Figs. 29–31)

REFERENCE: Hustedt (1959), p. 499, Fig. 924.

COMMENTS: Valves elliptical-lanceolate with sharply protracted apices 70–105 μm long, 30–38 μm wide. Axial area narrow, central area transapically expanded, joining a thin hyaline line not reaching the apex, on each side separating the one or two rows of transapically elongated areolae adjacent to the axial area from the rest. Each raphe branch is laterally inflated in the middle. Central striae shorter than the others; striae slightly radiate, 21–22 in 10 μm; areolae compactly arranged in longitudinal wavy lines, partecta uniform, rectangular 3–4 μm wide and 4–6 in 10 μm, reaching almost the apex of the valve. This species differs from *M. elegans* in the following features: (1) Partecta transapically rectangular and larger, (2) striae denser and, (3) central area joining a thin hyaline line on each side forming an "H"-shaped configuration. *Mastogloia elegans* has apically elongated partecta only 1 μm wide and the striae density is only 15 in 10 μm.

DISTRIBUTION: Present in small numbers in both subtidal and basin samples.

Mastogloia erythraea Grun.
(Fig. 32)

REFERENCES: Hustedt (1959), p. 524, Fig. 959; Stephens and Gibson (1980) J. Phycol. 16, 354–363.

COMMENTS: Length 40–65 μm, width 10–13 μm, striae 20–22 in 10 μm. Larger partecta one or two between the middle and the end on each side 2.5–3 μm wide and 2–4 μm long. Small partecta 1.5–2 μm wide and 1–2 μm long. Occasionally large partecta may be absent on one side.

DISTRIBUTION: Common in subtidal mats and the basin but rare in intertidal mats.

Mastogloia exigua Lewis
(Figs. 34, 35)

REFERENCE: Hustedt (1959), p. 569, Fig. 1003.

COMMENTS: Length 22–45 μm; width 9–15 μm, striae 20–22 in 10 μm, middle partecta large 3–5 in 10 μm; 1.5–2 μm wide; small partecta less than 1 μm wide; 4–6 in 10 μm. Two distinct forms were observed; one elliptic with protracted capitate ends and the other lanceolate, but the pattern of partecta and the striae are the same in both.

DISTRIBUTION: Common in the basin and subtidal mat, but very rare in the intertidal mat.

Mastogloia fimbriata (Bright W.) Cl.
(Fig. 36)

REFERENCES: Hustedt (1959), p. 465, Fig. 884; Stephens and Gibson (1979), Bot. Mar. 22:499–509.

COMMENTS: Length 42–75 µm; width 30–46 µm, striae 6–7 in 10 µm, partecta 5 µm wide and 7–9 µm long. Fresh habit of this diatom was found to show mucilage capsule and spine-like strands.

DISTRIBUTION: Found only in the subtidal mats.

Mastogloia aff. **foliolum** Brun.
(Figs. 37, 38)

REFERENCE: Hustedt (1959), p. 561, Fig. 993.

COMMENTS: Valves rhombic lanceolate with slightly produced blunt ends, 55–72 µm long, raphe branches deflected in the middle. Axial area narrow, central area transapically rectangular reaching almost half of valve face. Striae slightly radiate interrupted by a semilanceolate area of faintly arranged striae on each side. This area is demarcated by two longitudinal rows of areolae close to axial area and a striate zone reaching half of the valve face on the opposite side. Striae 21–24 in 10 µm. Partecta uniform, rectangular 5 in 10 µm, 2–2.5 µm wide. This taxon differs from *foliolum* in having uniform partecta and two transversely elongated areolae adjacent to the axial area and in its rhombic lanceolate shape. *Mastogloia foliolum* is lanceolate, and has larger partecti towards the middle and a single row of areolae adjacent to the axial area; otherwise features of these specimens are identical to *M. foliolum*.

DISTRIBUTION: Found mostly in the basin and rarely in the subtidal mats.

Mastogloia halophila John
(Figs. 39–41)

REFERENCES: John (1980), Nova Hedwigia 33:849–858; John (1983), p. 119, Pl. 50, Figs. 6, 7.

COMMENTS: Length 50–90 µm; width 17–20 µm, striae 16–17 in 10 µm, partecta 7–8 in 10 µm and 2–2.5 µm wide. This species was first described from a chain of hypersaline coastal lakes 100 km south of Perth in Western Australia. This can be easily distinguished from *M. lanceolata* Thwaites by the coarser striae and larger size range and from *M. aquilegiae* Grun. by its distinctly narrower partecta.

DISTRIBUTION: This species was the most commonly occurring diatom in all the samples, well distributed from intertidal, subtidal to deep basin of the Hamelin Pool. Variations in size and apices were common. The longer valves were mostly confined to the basin.

Mastogloia horvathiana Grun.
(Figs. 42, 43)

REFERENCE: Hustedt (1959), p. 471, Fig. 890.

COMMENTS: Length 47–96 µm; width 27–40 µm, striae 12–15 in 10 µm, partecta 4–6 in 10 µm; width 3.5–4 µm.

DISTRIBUTION: Rare; mostly found in the benthic microbial community at the basin.

Mastogloia ignorata Hustedt
(Figs. 44, 45)

REFERENCE: Hustedt (1959), p. 506, Fig. 932.

COMMENTS: Length 28–46 µm; width 10–15 µm, striae 22–25 in 10 µm, partecta 7–8 in 10 µm; width 2.5–3 µm.

DISTRIBUTION: Occurred predominantly in the subtidal mat and rarely in the basin.

Mastogloia inaequalis Cl.
(Fig. 46)

REFERENCE: Hustedt (1959), p. 566. Fig. 999b, c.

COMMENTS: Length 30–46 µm; width 10–11 µm, striae 25 in 10 µm, partecta 13 in 10 µm; larger partecti 1.5 µm wide; smaller ones 1 µm.

DISTRIBUTION: Very rare, observed only in subtidal mats.

Mastogloia labuensis Cl.
(Figs. 47–49)

REFERENCE: Hustedt (1959), p. 518, Fig. 950.

COMMENTS: Length 39–66 µm; width 15–18 µm, striae 16–18 in 10 µm, partecta 5–6 in 10 µm and 1.5–2 µm wide. (Hustedt reports 20–22 striae in 10 µm for this species and quotes Cleve's record of 15–17 in 10 µm, same as in the populations of Hamelin Pool.) SEM studies reveal that the areolae are small pores regularly arranged (Fig. 96). The smaller valves tend to have radiate striae at the center. Each raphe branch is deflected twice.

DISTRIBUTION: Occurred in large numbers and large size range along with *M. recta* in the benthic microbial communities as well as in the subtidal algal mats, but rarely in the intertidal mats.

Mastogloia lanceolata Thwaites
(Figs. 50, 51)

REFERENCES: Hustedt (1959), p. 497, Fig. 922; Stephens and Gibson (1980), Phycologia 19(2):143–152.

COMMENTS: Length 50–56 µm; width 18–22 µm, striae 20–22 in 10 µm, partecta 5 in 10 µm and 2 µm wide. The specimens in Hamelin Pool have all features reported in Hustedt, but not in Stephens and Gibson, who recorded a lower striae density (16–18 in 10 µm). However SEM structure (Fig. 98) is the same as that shown by Stephens and Gibson (1980), two silica ridges flanking the raphe.

DISTRIBUTION: Common in the benthic community in the basin and rare in the subtidal mats.

Mastogloia lineata Cl.
(Figs. 52, 53)

REFERENCE: Hustedt (1959), p. 538, Fig. 971.

COMMENTS: Length 65–82 µm; width 28–30 µm, striae 14 in 10 µm, partecta 7–8 in 10 µm and 1 µm wide.

DISTRIBUTION: Found in the benthic microbial community in the basin.

Mastogloia macdonaldii Grev.
(Figs. 54–57)

REFERENCE: Hustedt (1959), p. 560, Fig. 992.

COMMENTS: Length 45–50 µm; width 15–17 µm, striae 21–24 in 10 µm, partecta 4 in 10 µm and 2 µm wide. Two forms of this species were observed, one with protracted ends and the other with acute ends.

DISTRIBUTION: Found predominantly in the subtidal mats and rarely in the basin.

Mastogloia ovumpaschale (A. S.) Mann.
(Figs. 58, 59)

REFERENCE: Hustedt (1959), p. 477, Fig. 897.

COMMENTS: Length 52–74 µm; width 24–36 µm, striae 10–12 in 10 µm, partecta 3–5 in 10 µm and 2.5–3.5 µm wide.

DISTRIBUTION: Found predominantly in benthic sediment of the basin and rarely in the subtidal mat.

Mastogloia paradoxa Grun.
(Figs. 60, 61)

REFERENCES: Hustedt (1959), p. 519, Fig. 953; Stephen and Gibson (1980) Phycologia 19(2):143–152.

COMMENTS: Length 40–66 µm; width 11–16 µm, striae 25–26 in 10 µm, large partecta 4 in 10 µm and 1.5–2 µm wide; small partecta 6–7 in 10 µm; 1 µm wide; 1–3 large partecta in the middle.

DISTRIBUTION: Very common in the subtidal mat but rare in the intertidal mats and basin.

Mastogloia aff. **pseudoelegans** Hustedt
(Figs. 62–65)

REFERENCE: Hustedt (1955), p. 19, Pl. 6, Fig. 10.

COMMENTS: Valves broad elliptical to linear elliptical with acute rostrate apices or protracted blunt ends, 40–89 µm long and 20–26 µm wide. Raphe straight, axial area narrow and central area orbicular. Raphe slight deflected. Transapical striae slightly radiate towards the center and central striae short. Striae 18–20 in 10 µm. Partecta 2–3 µm wide; 6–7 in 10 µm, transapically rectangular. Puncta closely arranged in wavy longitudinal lines. This taxon resembles *M. apiculata* in general shape and striae, but lacks the silicified axial ribs on either side of the raphe as confirmed in SEM studies by Stephens and Gibson (1980). This also differs from *M. pseudoelegans* in having finer striae and high variation in shape ranging from very broad elliptical, similar to *M. citrus* Cl., to linear elliptical, like *M. pseudoelegans.*

DISTRIBUTION: Occurred in large numbers in the basin and in the subtidal samples.

Mastogloia perfecta Ricard
(Figs. 66, 67)

REFERENCE: Ricard, M. (1987), Fig. 773.

COMMENTS: Valve lanceolate to linear lanceolate with acute or slightly protracted blunt ends, 45–85 µm long, 16–28 µm wide. Raphe straight, axial area narrow, central area

broad, areolae in transapical and oblique lines; transapical striae 11–13 in 10 µm. Partecta narrow and apically elongated with concave inner margin, 2–3 in 10 µm and 1.5–2 µm wide. This taxon differs from *M. asperuloides* in having a larger central area and narrow apically elongated partecta with concave inner margins.

DISTRIBUTION: Occurred in the basin only.

Mastogloia punctifera Brun.
(Figs. 68–71)

REFERENCE: Hustedt (1959), p. 490, Fig. 914.

COMMENTS: Length 22–45 µm; width 11–16 µm, striae 20–21 in 10 µm, partecta 6–8 in 10 µm; width 2.5–3 µm. High variation in shape was observed and the size range is higher than previously reported for this species. The fresh cells of this species was ensheathed by concentric layers of mucilage forming capsules.

DISTRIBUTION: Most common in the subtidal mats and basin but rare in the intertidal mats.

Mastogloia pumila (Grun.) Cl.
(Figs. 72, 73)

REFERENCES: Hustedt (1959), p. 553, Fig. 983; John (1983) p. 121, Pl. 51, Figs 3–6.

COMMENTS: Length 20–28 µm; width 7–9 µm, striae 24–25 in 10 µm, large partecta 3–4 in 10 µm; 1.5–2 µm wide, small partecta 6 in 10 µm; 1 µm wide.

DISTRIBUTION: Common in subtidal mats, rare in intertidal mats.

Mastogloia pusilla Grun.
(Figs. 74, 75)

REFERENCE: Hustedt (1959), p. 568, Fig. 1002 (a–c).

COMMENTS: Length 20–35 µm, width 7–9 µm, striae 18–22 in 10 µm, middle large partectum (occasionally two) 1.5–2 µm wide and 2.5 µm long, small partecta 8 in 10 µm and less than 1 µm wide.

Mastogloia pusilla var. **linearis** Østrup.
(Figs. 76, 77)

REFERENCE: John (1983), p. 121, Pl. 51, Figs. 7, 8.

COMMENTS: Length 58–60 µm; width 10–11 µm, striae 20 in 10 µm, large partecta 1–3.5 µm long; 2 µm wide, small partecta 6 in 10 µm; 1.5 µm wide.

DISTRIBUTION: Common in subtidal mats, but rare in intertidal mats and the basin.

Mastogloia reimeri John
(Figs. 78–83)

REFERENCE: John (1980), Nova Hedwigia 33:849–858.

COMMENTS: Length 25–89 µm; width 9–19 µm, striae 16–17 in 10 µm. Partecta large 3–4 in 10 µm; 2–3 µm wide, partecta small 6–7 in 10 µm; 1–1.5 µm wide. This is distinguished from *M. braunii* by its narrower lanceolate to rhombic lanceolate shape, the "H"-shaped configuration of faint striae of transversely elongated areolae and coarser structure of areolae. This species was originally described from a chain of coastal hyper-

saline lakes in Western Australia (salinity range 50–132 ‰), but the present population includes smaller forms with a single enlarged partectum in the middle.

DISTRIBUTION: *Mastogloia reimerii* was one of the most common diatoms in Hamelin Pool. It was present in all samples.

Mastogloia recta Hustedt
(Figs. 84–87)

REFERENCE: Hustedt (1942), p. 42, Figs. 54–58.

COMMENTS: Length 32–90 µm; width 12–18 µm, striae 13–16 in 10 µm. Partecta 6–8 in 10 µm; width 3 µm. High variation in size and striae density were evident in this species.

DISTRIBUTION: Common in the benthic community and subtidal samples but the largest forms were in the basin.

Mastogloia singaporensis Voigt
(Figs. 88, 89)

REFERENCE: Voigt (1942), p. 17.

COMMENTS: Length 54–91 µm; width 14–20 µm, striae 28–30 in 10 µm, partecta 3–5 in 10 µm; width 2 µm.

DISTRIBUTION: Rare, subtidal and benthic only.

Mastogloia subaffirmata Hustedt
(Figs. 90, 91)

REFERENCE: Hustedt (1959), p. 527, Fig. 960 a–f.

COMMENTS: Length 25–50 µm; width 9–17 µm, striae 22 in 10 µm, partecta 10–14in 10 µm; width 2–2.5 µm.

DISTRIBUTION: Both elliptic lanceolate and rhombic lanceolate forms were common in the basin but rare in other samples.

Mastogloia varians Hustedt
(Figs. 92, 93)

REFERENCE: Hustedt (1959), p. 486, Fig. 909.

COMMENTS: Length 19–40 µm; width 7–10 µm, striae 18–20 in 10 µm, partecta apically elongated 4–6 in 10 µm; width 1–1.5 µm.

DISTRIBUTION: Common in the subtidal and intertidal mats, but rare in the basin.

Discussion

The species richness of *Mastogloia* observed in Hamelin Pool is one of the highest recorded for this genus in such a confined locality. Out of a total 80 taxa of diatoms encountered, 37 were *Mastogloia*. The actual number of species of *Mastogloia* might have been even higher had the sea grasses in Hamelin Pool been included in this study; many *Mastogloia* species are known to be epiphytic on sea grasses. Ricard (1974) recorded 50 taxa of *Mastogloia* from the lagoon of Vairoa in Tahiti. Foged (1975, 1984) recorded 48 taxa of *Mastogloia* out of 246 taxa of diatoms from the littoral coast of Tanzania and 56 out of 395 littoral taxa from Cuba. Navarro (1982) identified 25 taxa of *Mastogloia* among 226 marine diatoms associated with mangrove roots in the Indian River (salinity 16–42 ‰),

Florida. However Hustedt (1959) commented that a single mud sample from Miang Besan, Borneo contained about 60 *Mastogloia* species. He considered Indo-Malaysian islands as the center of high distribution of this genus. It appears that shallow, hypersaline marine environments in the tropical to sub-tropical regions tend to favor high diversity of this genus.

Certain clear trends emerged in the pattern of distribution of *Mastogloia* species. Among the three habitats investigated, the subtidal algal mat provided the maximum diversity of species. Virtually all the taxa described in this paper could be observed in subtidal samples whereas only 15 taxa were commonly found in the intertidal algal mats. The benthic microbial community at a depth of 4–7 m in the basin had a thriving population of 27 taxa of *Mastogloia*. The intertidal stromatolites are subjected to the most rigorous environmental turbulence of periodic desiccation and submergence by wave action. The normal spring tidal amplitude in Hamelin Pool ranges from 1 m to 0.6 m, and the diurnal amplitude ranges from 0.5 to 0.3 m (Playford and Cockbain 1976). The lowest diversity of *Mastogloia* species in the intertidal algal mat may be explained by the most unstable environment in this zone. The algal mat here is dominated by cyanobacteria and selected species of diatoms that include stalk-forming *Brachysira aponina* (John 1990), and some *Mastogloia* species.

Most of the intertidal stromatolites in Hamelin Pool are composed of particles of 125–250 μm size, lithified by aragonite cement (Logan et al. 1974). The subtidal stromatolites are made of even coarser sediment particles ranging from 500 to 5000 μm size and are more poorly laminated than the intertidal ones (Logan 1974). This may be attributed to the relative distribution of diatoms and green algae compared with that of cyanobacteria in the algal mats associated with these stromatolites. Diatoms and green algae due to their larger size are likely to trap and bind coarser particles. Most of the ancient and modern marine stromatolites elsewhere are finely laminated due to the trapping of finer particles by cyanobacteria and bacteria.

Among the diatoms encountered in Hamelin Pool, *Mastogloia* displayed the highest number of species with mucilage strands, capsules, and tubes. The other genera with copious mucus secretion were *Brachysira*, *Amphora*, *Berkeleya*, and *Climaconeis*. Prominent among the mucus-forming *Mastogloia* species were *M. cocconeiformis*, *M. cribrosa*, *M. angulata*, *M. pusilla*, *M. erythraea*, *M. punctifera*, *M. pumila*, and *M. fimbriata*. These species were represented predominantly in the algal mats associated with the subtidal stromatolites and to a lesser degree with the intertidal ones. The network of mucilaginous tubes produced by *M. cocconeiformis* with its profuse branching determined by the plane of cell division, and the competition by the growth of cohabiting green alga in the algal mat, *Cladophora*, appears to be unique among mucilage-producing diatoms. The dichotomously branching stalks produced by *Brachysira aponina* in Hamelin Pool (John 1990), *Cymbella*, and *Gomphonema* are different from the branching pattern of tubes produced by *M. cocconeiformis*. Mucilaginous secretion could be seen as a capsule as well as strands originating from the partectal chambers, coalescing into hollow tubes in the latter. The "tube-dwelling" diatoms, like some species of *Parlibellus*, *Navicula*, and *Gyrosigma*, have several cells in chains organized inside the mucilage tubes. In *M. cocconeiformis*, however, each frustule appears to secrete a single tube. The result is a profusely branching network, the base of each branch occupied by a frustule, integrating well with the green alga *Cladophora*. Stephens and Gibson (1979) have already demonstrated the presence of mucilaginous capsules or strands in *M. cribrosa*, *M. angulata*, *M. pusilla*, *M. erythreae*, *M. fimbriata*, and *M. pumila*. The size range of the mucilage capsules, strands, and tubes is quite conducive to trapping and binding of coarse particles, which

aid the accretion process of stromatolites. Winsborough and Seeler (1984) have demonstrated the role of diatoms in non-marine stromatolites.

Populations of largest size range of several species were confined to the benthic microbial community of the central basin of Hamelin Pool at a depth of 4–7 m. Prominent among these were *M. recta*, *M. halophila*, *M. labuensis*, *M. reimeri*, *M. decussata*, *M. angulata*, *M. asperula*, and *M.* aff. *asperuloides*. Stephens and Gibson (1979) pointed out that the same species may exist with or without mucous secretion. This appears to be the case in *M. angulata*, which occurred in the sediment of the basin in the largest size range without any apparent mucus strands. The basin probably provides the most stable environment without much competition for diatom growth. All the mucus secreting species were found in algal mats associated with mostly subtidal stromatolites. Though the algal mat provides an ideal substrate for *Mastogloia*, the competition offered by the prokaryotic cyanobacteria and the profusely branching green algae, coupled with constant deposition of sediment particles in a hypersaline environment, must be highly stressful. Metazoan herbivors are sparse in Hamelin Pool due to hypersalinity (Playford and Cockbain 1976). Copious mucus production even simulating the apparent morphology of a green alga such as *Cladophora*, as is the case with *M. cocconeiformis*, can be interpreted as a response to stressful environment, which might confer benefits of osmoregulation in a hypersaline environment. The vast diversity of *Mastogloia* species even in a small volume of algal mat epiflora on a subtidal stromatolite could be due to a relatively stressful—but stable and isolated—environment, ideal for evolution.

The high degree of variation found in certain taxa and the difficulty of delineating definite conservative criteria have made the determination of taxonomic status of some species challenging. For instance the systematic position of *M. asperula*, *M.* aff. *asperuloides*, *M. perfecta*, *M. ovumpaschele*, and *M. horvathiana*, all of which occurred in the central basin of Hamelin Pool, need to be further investigated. The structure of areola and parteeta is closely related in these taxa. The most widely distributed species were *M. halophila* and *M. reimeri*. The "riotous variation" alluded to by Paddock and Kemp (1988) in *Mastogloia* appeared to be more applicable to *M. reimeri* and *M. braunii* in Hamelin Pool than any other species. I am pursuing further investigation of these species along with others of ambiguous taxonomic status.

Acknowledgements

My sincere thanks to John Bauld of Canberra for collection of samples in 1983 and 1986 and to Janette Nowell of Curtin University for collection of samples in 1990 and for Figures 2 and 3. The typing of the manuscript by Melody Best (Curtin University) is gratefully acknowledged.

Literature Cited

BAULD, J. 1984. Microbial mats in marginal marine environments: Spencer Gulf, South Australia and Shark Bay, Western Australia. Pp 39–58 *in* Miocrobial mats: stromatolites, R. W. Castenholz, U. Cohen and H. O. Halvorson, eds. Alan Liss, New York.

DEXING, J., C. ZHAODI, S. JUNMIN LIN, AND L. HICHENG. 1984. Marine Benthic diatoms in China. China Ocean Press, Beijing.

EHRLICH, A. 1978. The diatoms of the hypersaline Solar Lake (Ne Sinai). Israel J. Bot. 27:1–13

FOGED, N. 1975. Some littoral diatoms from the coast of Tanzania. Bibl. Phycologica 16:1–127

———. 1978. Diatoms in Eastern Australia. Bibl. Phycologica 41:1–243

———. 1984. Freshwater and littoral diatoms from Cuba. Bibl. Diatomologica 5:1–243.

GOLUBIC, S. 1976. Organisms that build stromatolites. Pp. 113–126 *in* Stromatolites, Developments in Sedimentology 20, M. R. Walter, ed. Elsevier, Amsterdam.

HAGELSTIEN, R. 1938. The diatomaceae of Puerto Rico and the Virgin Islands. N. Y. Acad. Sci., Scientific Survey of Puerto Rico and Virgin Islands 8, Part 3:313–444.

HENDEY, N. J. 1964. An introductory account of the smaller algae of British coastal waters. Part V. Bacillariophyceae (Diatoms). H. M. S. O., London.

HOFFMAN, P. 1976. Stromatolite morphogenesis in Shark Bay, Western Australia. Pp 261–271 *in* Stromatolites, Developments in Sedimentology 20. M. R. Walter, ed. Elsevier, Amsterdam.

HUSTEDT, F. 1942. Süwasser-Diatomees des Indomalayischen Archipels und der Hawai-Inseln. Internat. Rev. Ges. Hydrobiol. Hydrogr. 42:1–252.

———. 1955. Marine littoral diatoms of Beaufort North Coastline. Duke Univ. Mar. Res. Sta. Bull. 6:1–67.

———. 1959. Die Kieselalgen Deutschlands Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeressgebiete, Teil 2. *In* Kryptogamen-Flora von Deutschland, Österreich und der Sweiz, L. Rabenhorst, ed. Otto Koeltz, Koenigstein.

JOHN, J. 1980. Two new species of the diatom *Mastogloia* from Western Australia. Nova Hedwigia 33:849–858.

———. 1983. The diatom flora of the Swan River estuary, Western Australia. Bibl. Phycologica 64:1–359.

———. 1990. Diatom flora of the microbial communities associated with stromatolites at Shark Bay, Indian Ocean, West Coast of Australia. Pp. 97–110 *in* Ouvragedédié à A. Germain, M. Ricard, ed. O. Koeltz, Koenigstein.

LOGAN, B. W. 1974. Inventory of diagenesis in Holocene-Recent carbonate sediments Shark Bay, Western Australia. Am. Assoc. Petrol. Geol. Mem. 22:195–249.

LOGAN, B. W., P. HOFFMAN, AND C. D. GEBELEIN. 1974. Algal mats, cryptalgal fabrics and structures Hamelin Pool, Western Australia. Am. Assoc. Petrol. Geol. Mem. 22:140–194.

NAVARRO, J. N. 1982. Marine diatoms associated with Mangrove prop roots in the Indian River, Florida. U. S. A. Bibl. Phycologica 61:37–42.

NOVARINO, G. 1989. An update of the taxa of the genus *Mastogloia* with a resemblance list for the more recently described ones. Diatom Res. 4:319–343.

PADDOCK, T. B. B. AND K. D. KEMP. 1988. A description of some new species of the genus *Mastogloia* with further observations of *M. elegans* and *M. goessi*. Diatom Res. 3:109–121.

PATRICK, R. M., AND C. W. REIMER. 1966. The diatoms of the United States. Acad. Nat. Sci. Phila. Monograph No. 13. 688 pp.

PERAGALLO, H. AND M. PERAGALLO. 1897–1908. Diatomees marines de France et des Districts maritimes voisins. M. J. Tempère, Grez-sur Loing.

PLAYFORD, P. E. AND A. E. COCKBAIN. 1976. Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia. Pp. 389–411 *in* Stromatolites, Developments in Sedimentology 20, M. R. Walter, ed. Elsevier, Amsterdam.

RICARD, M. 1974. Etude taxiunomique des diatomées marines due lagon de Vairao (Tahiti). 1. Le genre *Mastogloia*. Rev. Algol. N. S. 11:161–177.

———. 1987. Atlas du phytoplankton marin Diatomophycées. Centre National de la Rocherche Scientifique, Paris.

SCHMIDT, A. 1874–1959. Atlas der Diatomaceen-kunde. Plates 1–480. R. Reisland, Leipzig.

SIMONSEN, R. 1987. Atlas and catalogue of the diatom types of Friedrich Hustedt. 3 Vols. J. Cramer, Berlin.

STEPHENS, C. F. AND R. A. GIBSON. 1979. Ultrastructural studies on some *Mastogloia* (Bacillariophyceae) species belonging to the group Ellipticae. Bot. Mar. 22:499–509.

———. 1979. Observations of loculi and associated extracellular material in several *Mastogloia* (Bacillariophyceae) species. Rev. Algol. N. S. 14:21–32.

———. 1980. Ultrastructural studies of some *Mastogloia* (Bacillariophyceae) species belonging to the group Sulcatae. Nova Hedwigia 33:219–248.

——— 1980. Ultrastructural studies on some *Mastogloia* species of the group Inaequales (Bacillariophyceae). J. Phycol. 16:354– 363.

VOIGT, M. 1942. Contribution to the knowledge of the diatom genus *Mastogloia*. J. R. Microsc. Soc. 62:1–20.

WINSBOROUGH, B. M. AND J. S. SEELER. 1984. The relationship of diatom epiflora to the growth of limnic stromatolites and microbial mats. Pp 395–407 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard, ed. O. Koeltz, Koenigstein.

WOOD, E. J. F. 1963. Check list of diatoms recorded from the Indian Ocean. CSIRO, Div. Fish. Oceanog., Rep. 36. Mar. Lab. Cronulla, Sydney.

Explanation of Plates

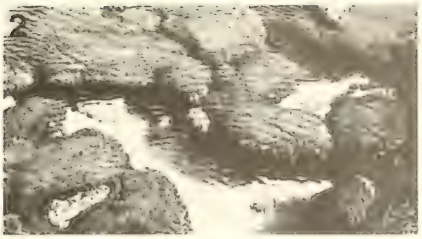
Plate 1, Figures 2–6
FIGURE 2. Intertidal stromatolites. FIGURE 3. Subtidal stromatolites at 3.5 m depth. FIGURES 4–6. LM. Scale bar = 10 µm. FIGURE 4. Fresh cell of *Mastogloia pumila* with concentric layers and terminal strands of mucilage. FIGURE 5. Fresh growing habit of *M. cocconeiformis* with mucilage tubes made of tiny strands. A new tube is formed from every frustule. FIGURE 6. Disintegrated mucilage tube of the above species showing individual strands.

Plate 2, Figures 7–28
FIGURES 7–28. LM. Scale bar = 10 µm. FIGURES 7–9. *Mastogloia angulata*. FIGURES 10–12. *M. asperula*. FIGURES 13–15. *M.* aff. *asperuloides*. FIGURES 16, 17. *M. baldjikiana*. FIGURE 18. *M. binotata*. FIGURES 19, 20. *M. braunii*. FIGURES 21, 22. *M. cocconeiformis*. FIGURES 23, 24. *M. corsicana*. FIGURE 25. *M. cribrosa*. FIGURE 26. *M. crucicula*. FIGURES 27, 28. *M. decussata*.

Plate 3, Figures 29–57
FIGURES 29–57. LM. Scale bar = 10 µm. FIGURES 29–31. *M.* aff. *elegans*. Fig. 32. *M. erythraea*. FIGURES 33–35. *M. exigua*. Fig. 36. *M. fimbriata*. FIGURES 37, 38. *M.* aff. *foliolum*. FIGURES 39–41. *M. halophila*. FIGURES 42, 43. *M. horvathiana*. FIGURES 44, 45. *M. ignorata*. FIGURE 46. *M. inaequalis*. FIGURES 47–49. *M. labuensis*. FIGURES 50, 51. *M. lanceolata*. FIGURES 52, 53. *M. lineata*. FIGURES 54–57. *M. macdonaldii*.

Plate 4, Figures 58–93
FIGURES 58–93. LM. Scale bar = 10 µm. FIGURES 58, 59. *M. ovumpaschale*. FIGURES 60, 61. *M. paradoxa*. FIGURES 62–65. *M.* aff. *pseudoelegans*. FIGURES 66, 67. *M. perfecta*. FIGURES 68–71. *M. punctifera*. FIGURES 72, 73. *M. pumila*. FIGURES 74, 75. *M. pusilla*. FIGURES 76, 77. *M. pusilla* var. *linearis*. FIGURES 78–83. *M. reimeri*. FIGURES 84–87. *M. recta*. FIGURES 88, 89. *M. singaporensis*. FIGURES 90, 91. *M. subaffirmata*. FIGURES 92, 93. *M. varians*.

Plate 5, Figures 94–99
FIGURES 94–99. SEM. Scale bar = 10 µm. FIGURE 94. *M. asperula*. Internal surface of the valve showing the circular areolae in oblique lines. FIGURE 95. *M.* aff. *asperuloides*. External surface view of valve showing circular areolae in oblique lines. Note transapically elongated row of areolae adjacent to the axial area. FIGURE 96. *M. labuensis*. External surface view showing double deflection of raphe and the structure of areolae. FIGURE 97. *M. recta*. External surface view. Note the double high deflection of the raphe branch and the circular areolae. FIGURE 98. Internal surface view of *M. lanceolata*. Note the silica ridges flanking the raphe. FIGURE 99. *M. punctifera*. External surface view with the highly sinuous raphe, longitudinal and transverse ridges separating the areolae, and the partectal pores.

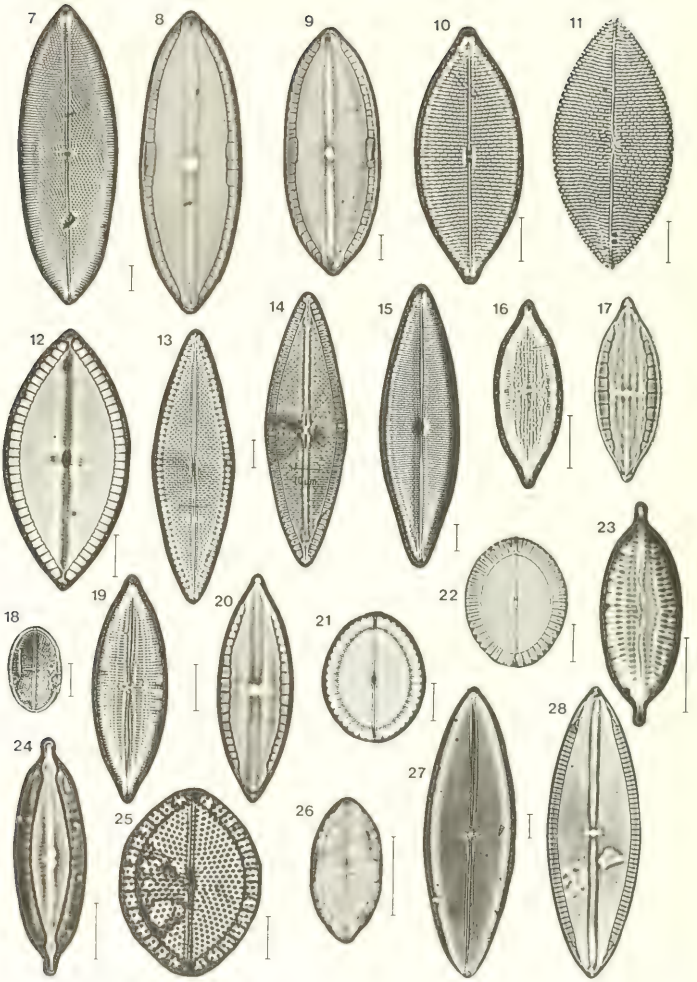

2

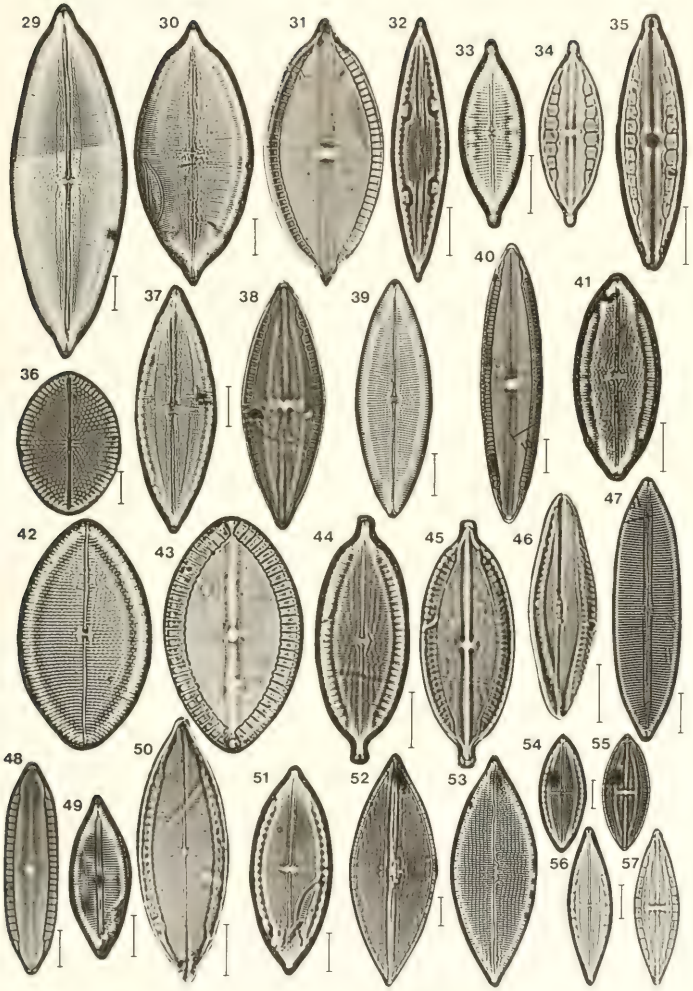
3

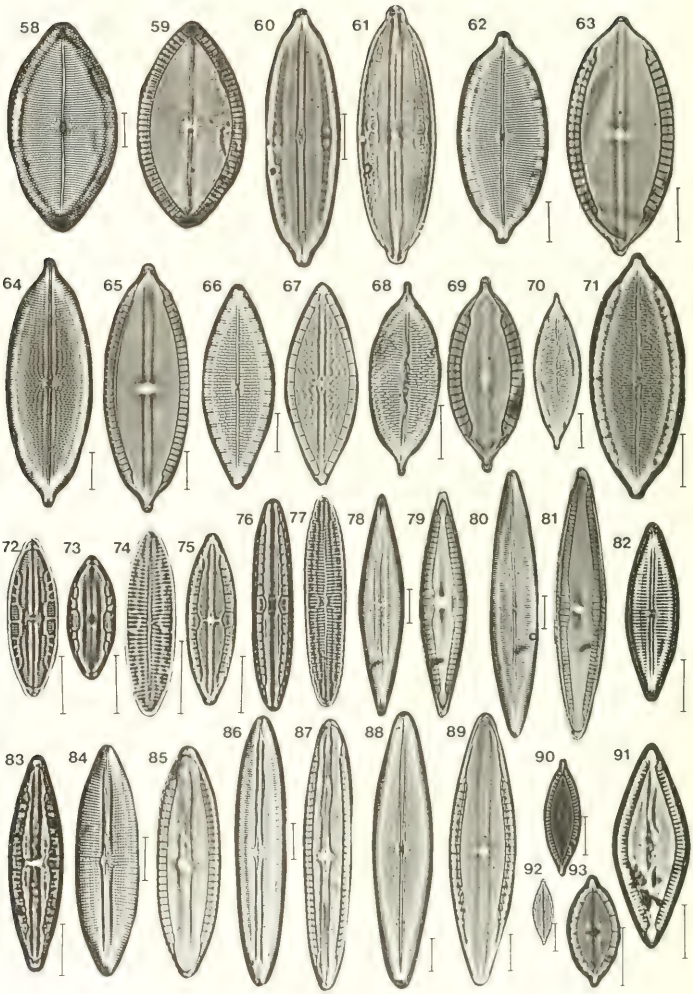
5

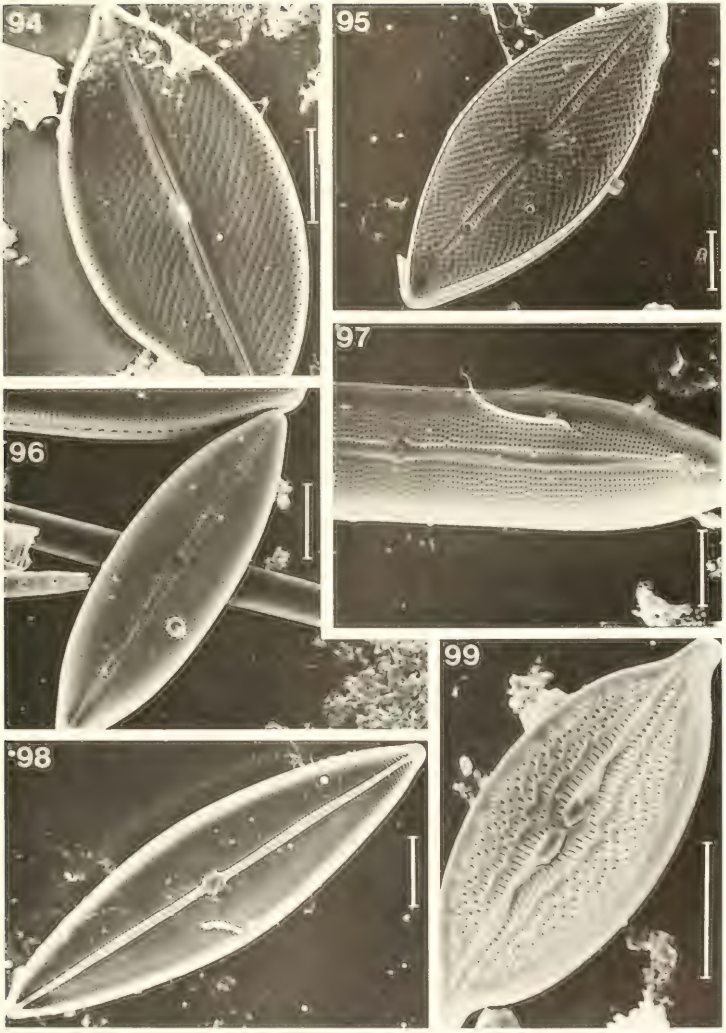
4

6


7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28


29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57


58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93


94
95
97
96
99
98

Examination of Type Material of *Denticula rainierensis* Sovereign

by

Jeffrey R. Johansen and Sal La Cognata

Department of Biology, John Carroll University,
University Heights, Ohio 44118

and

John P. Kociolek

Department of Invertebrate Zoology and Geology, California Academy of Sciences,
Golden Gate Park, San Francisco, California 94118

With 1 table and 3 plates

Abstract: Populations of a small, finely striate *Denticula* were found in samples from a winter seep wall community associated with Chagrin Falls on the Chagrin River in northern Ohio. The species at first was thought to be a new taxon most similar to *D. rainierensis* Sovereign. However, upon examining type material of *D. rainierensis* we found that our specimens were identical to Sovereign's specimens, which had been incorrectly described. We now emend the description of this species as follows: length 8–16 µm; width 2–4 µm; costae more or less radiate at the apices, 8–10 in 10 µm; striae 45–52 in 10 µm (rather than 26–30 in 10 µm as originally stated); otherwise as stated in the original description. Others have suggested synonymy between *D. rainierensis* and *D. subtilis* Grunow. At present we question this proposed synonymy since published light micrographs of type material of *D. subtilis* have more acute apices, lack radiate costae, and are reported to have 28–30 striae in 10 µm. Distributional differences between the taxa also exist, with *D. rainierensis* occurring typically in freshwater subaerial habitats and shallow hot springs, while *D. subtilis* has most often been collected from brackish estuarine waters.

Introduction

Two finely striate, inland *Denticula* species have been described, *D. subtilis* Grunow and *D. rainierensis* Sovereign. These species overlap in reported striae density (28–30 in 10 µm, 26–30 in 10 µm, respectively), costae density (6–9 in 10 µm, 8–10 in 10 µm, respectively), and size (8–20 µm by 2–3 µm, 12–15 µm by 2–3 µm, respectively). Lange-Bertalot and Krammer (1987) consider *D. rainierensis* a later synonym of *D. subtilis* and designate a lectotype for the earlier species.

We have recently begun study on a seep wall associated with Chagrin Falls on the Chagrin River in northeastern Ohio. In our first collections from the wall, we found an unusual *Denticula* species that differed from most freshwater species in the genus by its lack of striae visible in the light microscope. Examination under both transmission and scanning electron microscopes indicated that striae density was finer than that observed in any previously described species of the genus. However, striking similarities between our taxon and *D. rainierensis* were noted, and we subsequently examined type material of *D. rainierensis* collected from Ohanapecosh Hot Springs in Mt. Ranier National Park, Washington (Sovereign 1963). Our examination showed that the *Denticula* species from Chagrin Falls was indeed *D. rainierensis*, and that the original description of this taxon was incorrect. This paper presents the results of our study of type and Chagrin Falls material of *D. rainierensis* in light and electron microscopes. The description is emended, and the proposed synonymy with *D. subtilis* is discussed.

Materials and Methods

Samples were collected from December 1988 to October 1989 from the steep, south-facing bank of the Chagrin River from seeps in the shale substrate both above and below Chagrin River Falls in the village of Chagrin Falls, Cuyahoga County, Ohio. Samples were boiled in nitric acid, washed in distilled water, and air dried onto coverslips. The coverslips were either mounted in Naphrax resin for light microscopy or attached to aluminum stubs for scanning electron microscopy (SEM). Slides were examined on an Olympus BH2 photomicroscope with Nomarski DIC optics. Stubs bearing material were sputter-coated with approximately 20 nm of gold-palladium, and viewed with a JEOL T100 scanning electron microscope at an operating voltage of 10 kV.

Diluted samples were also mounted on formvar-coated, hexagonal, copper grids for transmission electron microscopy (TEM). Grids were examined on a JEOL 100CX transmission electron microscope at an operating voltage of 80 kV.

The holotype slide and cleaned pellet material from Ohanapecosh Hot Springs were obtained from the Sovereign Diatom Collection (Mahood 1978, slide 426-4, Holotype no. 3499), housed at the California Academy of Sciences. Pellet material was recleaned and mounted on stubs for SEM study following the methods described above. Type material was studied on a JEOL 840A scanning electron microscope at an operating voltage of 15 kV.

Results

Denticula rainierensis was rare in the type material, making up 0.8 % of the total diatom community (based on a count of 1000 valves). Additionally, in SEM most valves appeared eroded. For this reason most of our results will be based upon micrographs of *D. rainierensis* from Chagrin Falls as the taxon was both abundant (Table 1) and in an excellent state of preservation in this material. Both populations shared several common traits, including size, striae and costae density, shape, orientation of the costae, and internal ultrastructure of costae. Considerably more morphological variation with regard to shape was noted in the Chagrin Falls population, likely due to the greater number of valves that were observed.

In typifying *D. rainierensis* Sovereign (1963) designated a holotype that was atypical for the species (Fig. 1). The specimen appears to have a salt or acid halo and is at the small end of the size range. He may have chosen this valve because the costal thickenings proximal to the raphe are clearly visible, although it was, in our opinion, an unfortunate choice since it is unlike any other specimen of the species in the type material. Other

TABLE 1. Percent density of *D. rainierensis* in diatom strew mounts of samples from Chagrin falls 12/88–10/89.

Site	Dec.	Mar.	June	Aug.	Oct.
Above falls, seep wall	19	0	3	1	4–5
Above falls, shoreline	6	43	0	0	12
Above falls, midstream	0	0	0	1	0
Below falls, seep wall	3–52	2	2	2	2–3

specimens appear similar to the holotype (Figs. 2, 3), but even more similar to medium-sized specimens in the Chagrin Falls material (Figs. 5–10). Striae are unresolved in all specimens. Very faint refraction patterns parallel to the costae were visible occasionally on the margins of the valve, and we assume these are what were counted as striae.

Valves are typically linear-lanceolate with acutely rounded apices (Figs. 1–10, 13–15, 17–21), although valves with a more linear-elliptical shape and broadly rounded ends are not uncommon in the large population at Chagrin Falls (Figs. 11, 12). The ends of the costae are not capitate in girdle view (Fig. 16), and thus differ from those in *D. elegans* Kützing and *D. thermalis* Kützing (Patrick and Reimer 1975).

The raphe is marginal along the edge of the valve face. Proximal raphe ends are 0.2–0.3 µm apart and are not deflected or branched (Fig. 26). Distal raphe ends are deflexed towards the proximal margin (Fig. 27). Internally, the raphe lies in the raphe canal and is generally difficult to observe (Figs. 24, 28). However, rarely the raphe will be formed in a less eccentric position, in which case both the raphe and raphe canal are clearly visible (Fig. 31). When the raphe is in this latter position, marginal ribs visible in both LM and SEM often develop on the valve mantle adjacent to the raphe (Figs. 4, 12, 31).

Costae are typically parallel to one another in the center of the valve, becoming slightly to distinctly radiate with respect to the raphe towards the ends (Figs. 1–14, 17–19). When viewed externally in SEM the costae are narrowest near the margin opposite the raphe (Figs. 22, 23). Internally costae have the greatest height and width near the margins (Figs. 24, 29). Costae are thickened at both margins (Figs. 24, 28–30), often more so along the raphe-bearing margin than on the opposite side (Fig. 29). These costal thickenings form a ridge-like structure along each side of the valve, which is most clearly visible in oblique view (Fig. 30).

The copula bears very narrow septa that match the frequency and width of the costal thickenings, and we assume these septa cover the internal margins of the costae in intact frustules (Fig. 25). In addition to the septa, the open copula also bears a single row of puncta along each side. Pleurae lack any pores or ornamentation (Fig. 22).

Striae consist of simple pores arranged in irregular rows parallel to the neighboring costae (Figs. 17–20, 22, 23). Striae extend from the mantle edge across the valve face to the axial area bearing the raphe, and continue as small pore fields on the other side of the raphe (Figs. 22, 26, 27). The valve face has 45–52 striae in 10 µm, the variability due to irregularity of striae formation as well as density of costae.

Discussion

In their discussion of *D. subtilis*, Krammer and Lange-Bertalot (1988) state that *D. rainierensis* is probably a later synonym of *D. subtilis* due to the similarity of size, costae density, striae density, and shape. Although a close relationship between these taxa is likely, we do not feel that at present they should be considered synonymous. The type

specimen of *D. subtilis* (Lange-Bertalot and Krammer 1987:231) has very acute ends and costae that are parallel throughout. Other specimens from the type material (Krammer and Lange-Bertalot 1988, Figs. 2, 3) also have acute ends and parallel costae. *D. rainierensis* differs by having bluntly rounded to wedge-shaped apices, generally a smaller length-width ratio, and costae that are radiate at the apices.

Although striae density for *D. subtilis* is reported as 28–30 in 10 µm, the valves consistently appear hyaline, and electron microscopical study of this taxon is necessary to determine an accurate density range. At present, *D. rainierensis* has finer striae than that reported for *D. subtilis*. Krammer and Lange-Bertalot (1988, Figs. 4–9) show specimens of *Denticula* from the Rio Ulla in northern Spain that actually belong to *D. rainierensis*. Mann (1984) shows SEM micrographs of internal valve surfaces of *D. rainierensis* from unspecified sites.

Some marine *Denticula* species also have fine striae (*D. hyalina* Schrader and *D. seminae* Simonsen and Kanaya), but all marine taxa have been transferred to other genera, namely *Crucidenticula* Akiba et Yanagisawa (1985), *Denticulopsis* Simonsen (1979), and *Neodenticula* Akiba et Yanagisawa (1985). With the exception of *Neodenticula seminae* (Sim. et Kan.) Akiba et Yanagisawa, all species of these marine genera are extinct fossil taxa.

At Chagrin Falls, *D. rainierensis* occurred most frequently associated with *Urococcus hookerianus* (Hass.) Kützing on south-facing seep walls both above and below Chagrin Falls. It also occurred at the shoreline above the falls, in seep wall samples lacking *Urococcus*, and rarely in midstream above the falls. The diatom was most abundant during cold weather, possibly because *Urococcus* died out once the weather warmed (Table 1). The ecological preference of this taxon would appear to be within mucilage of other algae in cold, subaerial habitats based upon our observations in Ohio. It is interesting that the type locality is a warm spring with water temperatures of 23° C. A seep wall is similar to a hot spring in that water temperatures can be very elevated during sunny days due to the ability of the sun to heat the thin layer of slow moving water that dampens the seep wall. Mucilaginous algae also typically inhabit both sites. Other *Denticula* species, such as *D. elegans* f. *valida* Pedicino also are known to occur in both hot springs and seep walls (Patrick and Reimer 1975, Johansen et al. 1983a, 1983b). It is interesting to note that the ecological preference of *D. subtilis* is the brackish waters of estuaries (Patrick and Reimer 1975), indicating that physiological differences between the two taxa also exist.

Other diatoms associated with *D. rainierensis* in the Chagrin Falls material include a number of taxa previously reported from subaerial seep walls (Johansen *et al.* 1983a, 1983b; Rushforth *et al.* 1976, 1984), including: *Achnanthes lanceolata* Breb., *A. linearis* W. Sm., *Amphora coffeiformis* (Ag.) Kütz., *A. ovalis* var. *pediculus* (Kütz.) V.H., *Caloneis bacillum* var. *fontinalis* Grunow, *Cymbella microcephala* Grunow, *Epithemia argus* var. *protracta* Mayer, *Gomphonema olivaceum* (Lyngb.) Kütz., *Navicula cincta* var. *heufleri* Grunow, *N. gallica* (W. Sm.) V.H., *N. subbacillum* Hust., *Nitzschia communis* Rabenh., *N. frustulum* (Kütz.) Grunow, *N. hantzschiana* Rabenh., *N. inconspicua* Grunow, *N. pusilla* (Kütz.) Lange-Bertalot, *N. tryblionella* var. *debilis* (Arnott) Mayer, and *N. valdestriata* Aleem et Hust.

Denticula rainierensis, Sovereign emend Johansen et. al.

Emended Description. Frustulum rectangulare in aspectu cingulari. Copula serie singulari punctorum et septa perangusta. Valva linearilanceolata contracta ad apices acute vel aliquando late rotundatos, 8–16.5 µm longa, 2.3–4 µm lata. Raphe prope marginem et invisibilis in microscopium lucem; raphes in marginibus oppositis frustuli. Costae 8–10 in 10 µm. Extrema costarum non clare capitati in aspectu cingulari. Striae subtiliter punctatae compositae serietum punctorum irregularium, 45–52 in 10 µm.

Frustule rectangular in girdle view. Copula with a single row of puncta and very narrow septa. Valve linear-lanceolate, tapering to acutely rounded or occasionally broadly rounded apices, 8–16.5 µm long by 2.3–4 µm wide. Raphe near the margin and not visible in the light microscope; raphes on opposing margins of the frustule. Costae 8–10 in 10 µm. Ends of costae as seen in girdle view not clearly capitate. Striae finely punctate, composed of irregular rows of puncta, 45–52 in 10 µm.

Acknowledgements

Joseph Polak operated the transmission electron microscope and the JOEL 840A scanning electron microscope. Tom Knobloch provided darkroom assistance. Funding for this project was provided by the Committee for Research and Service, John Carroll University.

Literature Cited

AKIBA, F. AND Y. YANAGISAWA. 1985. Taxonomy, morphology and phylogeny of the Neogene diatom zonal marker species in the middle-to-high latitudes of the North Pacific. Pp. 483–554 *in* Initial Reports of the Deep Sea Drilling Project, Vol. 87, H. Kagami, D. E. Karig, and W. T. Coulbourn eds. U. S. Gov. Printing Office, Washington, D. C.

JOHANSEN, J. R., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1983a. The algal flora of Navajo National Monument, Arizona, U. S. A. Nova Hedwigia 38:501–553.

JOHANSEN, J. R., S. R. RUSHFORTH, R. OBERNDORFER, N. FUNGLADDA, AND J. A. GRIMES. 1983b. The algal flora of selected wet walls in Zion National Park, Utah, U. S. A. Nova Hedwigia 38:765–808.

KRAMMER, K. AND H. LANGE-BERTALOT. 1988. Bacillariophyceae. Part 2: Bacillariaceae, Epithemiaceae, Surirellaceae. Band 2 *in* Suesswasserflora von Mitteleuropa. H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fischer, Jena. 596 pp.

LANGE-BERTALOT, H. AND K. KRAMMER. 1987. Bacillariaceae, Epithemiaceae, Surirellaceae: neue und wenig bekannte Taxa, neue Kombinationen und Synonyme sowie Bemerkungen und Erganzungen zu den Naviculaceae. Bibliotheca Diatomologica 15:1–289.

MAHOOD, A. 1978. The Harry E. Sovereign Collection of Northwest Pacific diatoms. Proc. Cal. Acad. Sci. 41(13):339–343.

MANN, D. G. 1984. An ontogenetic approach to diatom systematics. Pp. 113–144 *in* Proceedings of the Seventh Symposium on Recent and Fossil Diatoms, D. G. Mann, ed. Otto Koeltz, Koenigstein.

PATRICK, R. AND C. W. REIMER. 1975. The Diatoms of the United States, Volume 2, Part 1. Monograph No. 13. Acad. Nat. Sci. Philadelphia. 213 pp.

RUSHFORTH, S. R., I. KACZMARSKA, AND J. R. JOHANSEN. 1984. The subaerial diatom flora of Thurston Lava Tube, Hawaii. Bacillaria 7:135–157.

RUSHFORTH, S. R., L. L. ST. CLAIR, T. A. LESLIE, AND D. A. ANDERSON. 1976. The algae of two hanging gardens from southeastern Utah. Nova Hedwigia 27:231–323.

SIMONSEN, R. 1979. The diatom system: ideas on phylogeny. Bacillaria 2:9–97.

SOVEREIGN, H. E. 1963. New and rare diatoms from Oregon and Washington. Proc. Calif. Acad. Sci., Ser. 4, 31(14):349–368.

Explanation of Plates

Plate 1, Figures 1–21

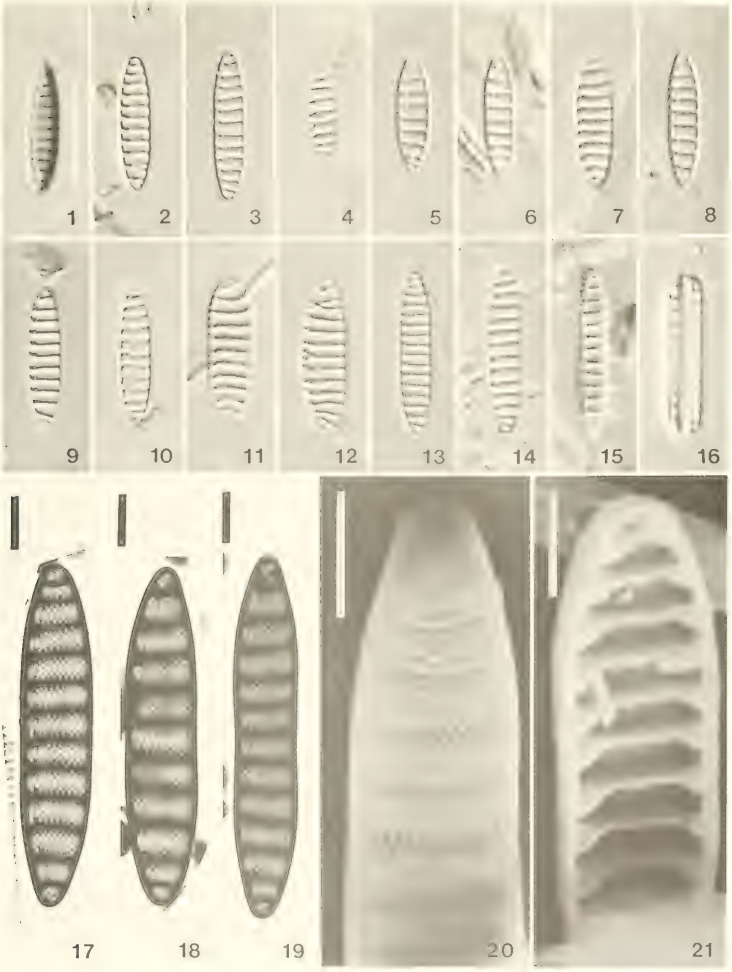
Figures 1–21. *D. rainierensis*. Figs. 1–16. Light micrographs showing variation in size and costae density, scale = 10 µm. Fig. 1. Holotype specimen from Ohanapecosh Hot Springs. Figs. 2, 3. Additional specimens from type locality. Figs. 4–16. Specimens from Chagrin Falls locality. Figs. 17–21. Scale = 2 µm. Figs. 17–19. TEM micrographs showing striae density (Chagrin Falls). Fig. 20. SEM micrograph of valve face, raphe lies on left-hand side of valve but is not visible at angle shown (Ohanapecosh). Fig. 21. SEM micrograph of internal structure of valve (Ohanapecosh).

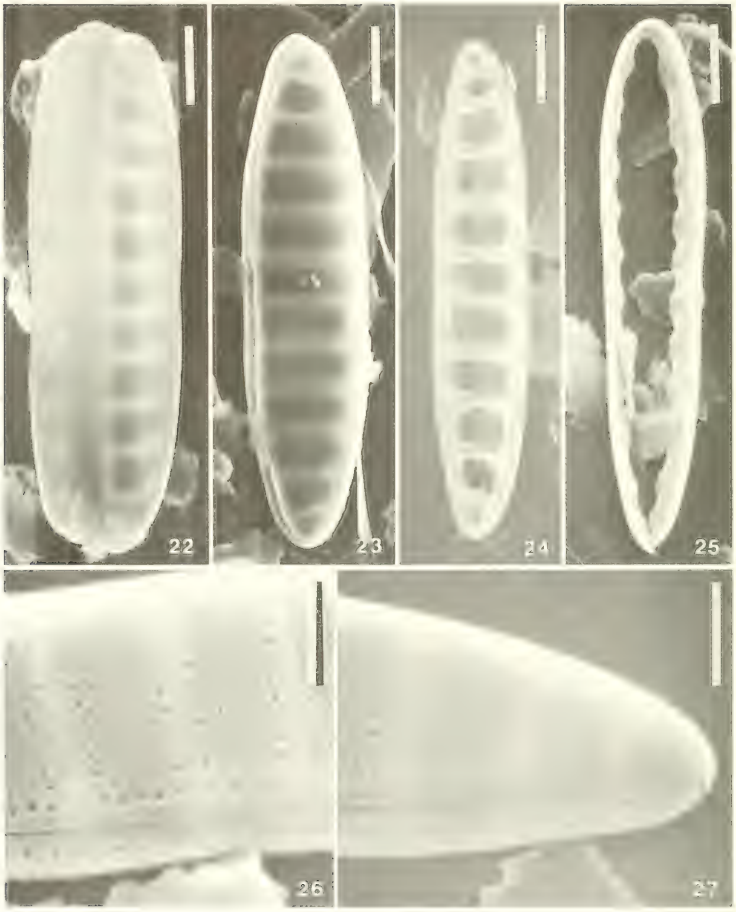
Plate 2, Figures 22–27

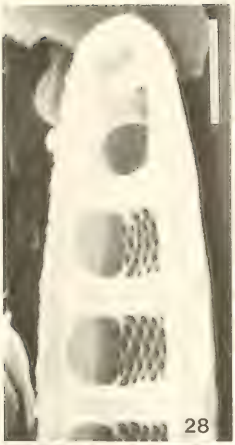
Figures 19–24. *D. rainierensis* from Chagrin Falls, December 1988, in SEM. Figs. 22–25 Scale = 2 µm. Figs. 22, 23. External views of frustule; raphe is on the right-hand side of both frustules. Fig. 24. Internal view of valve. Fig. 25. Girdle band with single opening. Figs. 26, 27. Scale = 1 µm. Fig. 26. Proximal raphe ends; note puncta on the mantle. Fig. 27. Distal raphe end.

Plate 3, Figures 28–31

Figures 28–31. Internal views of *D. rainierensis* in SEM. Scale = 1 µm. Fig. 28. Apex of valve; note raphe slit and distal raphe end (Chagrin Falls). Fig. 29. Valve showing striae and elevations of the costae; the raphe lies on the lower margin, but is not visible at angle shown (Ohanapecosh). Fig. 30. Oblique view of internal valve surface showing shoulder-like elevations of the costae (Chagrin Falls). Fig. 31. Aberrant valve with raphe set in from the margin (Chagrin Falls).


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21


22
23
24
25
26
27


28

29

30

31

Morphology, Cytology, and Growth Characteristics of the Diatom *Planktoniella sol* (Wall.) Schütt

by

P. E. Hargraves

Graduate School of Oceanography, University of Rhode Island,
Narragansett, Rhode Island 02882

and

A. M. Schmid

Institut für Pflanzenphysiologie, Universität Salzburg,
Hellbrunner Str. 34, A-5020 Salzburg, Austria

with 1 figure, 1 table, and 4 plates

Abstract: The planktonic diatom *Planktoniella sol* is widely distributed in oceanic waters throughout the world. Its most obvious characteristic is a circumferential "wing" of organic material, presumably polysaccharide. It superficially resembles species of *Thalassiosira*, particularly *T. eccentrica*, although it also exhibits a variety of morphological features that separate it from related taxa. Ultrastructural observations suggest that the wing may be a result of vesicles produced in Golgi bodies, extruded through the valvocopula rather than through the valvar processes. Interclonal growth variability is apparent at a variety of temperatures, although growth is negligible below 15° C and above 30° C.

Introduction

Planktoniella is a widespread genus in warmer seas with a small number of species. Two of the species listed as valid by VanLandingham (1978) are poorly known and may not be sufficiently distinct (*P. formosa* (Schimp. *ex* Karst.) Karst. and *P. florea* Wood, Crosby et Cassie) to warrant specific status, and *P. muriformis* (Loeblich, Wight et Darley) Round is a colonial form apparently found only in tropical and subtropical coastal waters (Round, 1972 and PEH, pers. obs.). The most common and cosmopolitan form is *P. sol* (Wallich) Schütt, a distinctive unicellular species mostly distributed in oceanic waters except when transported inshore by currents. It has been characterized as eurythermal and stenohaline, and as an indicator of Gulf Stream intrusion into the Norwegian Sea (Smayda 1958).

It has been noted in the literature that *Planktoniella sol* is closely related to *Thalassiosira* (e.g., Karsten 1928), and that the generically unique "wing" in this species is morphologically associated with the epitheca, implying a formative relationship. The availability of preserved material from different parts of the world, and the isolation of the species into culture, provided the incentive to investigate the growth habits, morphology, and cytology of this attractive diatom.

Materials and Methods

Microscopic observations are based on preserved material from Baja California (ca. 27° N, 114° W) and the Agulhas Passage (ca. 35–38° S, 20–25° E). Clones C26 and C40 were isolated from Baja California material (PEH); and a "Pacific" clone (J. Jordan to AMS) was used for some microscope observations as well as for APM (amiprophos-methyl) treatment according to the technique of Schmid (1984b). Maintenance of cultures and growth rate experiments were in 'f/2' medium (Guillard 1975). Growth experiments were conducted in stationary 125 ml flasks and counted in a Sedgewick-Rafter chamber (Guillard 1973). Temperature precision was 1° C; "high" light was 300 $\mu E \cdot m^{-2} \cdot sec^{-1}$ PFD, "low" light was 40 $\mu E \cdot m^{-2} \cdot sec^{-1}$. The clones are no longer extant.

For LM, cells were untreated or washed in 30 % H_2O_2 or SDS cleaned (Schmid and Schulz 1979), stained with 1 % solution of Toluidine blue in 50 % isopropyl alcohol, and photographed with a Reichert Zetopan or Zeiss Photomicroscope II. For SEM, cells were washed free of salt in deionized water with or without oxidation in cold sulfuric-nitric acid or 30 % H_2O_2, coated with Au-Pd and examined in a JEOL JSM-U3 or 1200 EX. For TEM, centrifuged cells were fixed in 2 % glutaraldehyde followed by 1 % osmium, embedded in Spurr's resin, sectioned, post-stained with uranyl acetate and lead citrate, and examined in a Zeiss EM-9S/2.

Results

Morphology

The general EM features of valve structure have been discussed previously by Gerloff (1970), Fryxell and Hasle (1972), Round (1972), Hallegraeff (1985) and Round et al. (1990). Morphological observations by light microscopy are found in, among others, Cupp (1943) and Gerloff (1970). Some photos in the latter paper are probably *Thalassiosira* or *Coscinodiscus* rather than *P. sol*.

The pattern of areolae on the valve is tangential (Figs. 1–4, 12, 13) except teratological cells, which show an irregular fasciculate pattern (Fig. 5). The circumferential wing is composed of many radially arranged chambers fused together. In living cells the chambers are liquid-filled and up to 7 μm in thickness (Fig. 7). The orientation of the individual chambers is possibly mediated by microtubule activity: in stressed cells in culture (Figs. 2–4) and treated with the microtubule-inhibiting herbicide APM (Figs. 5, 6), the cohesion of the chamber segments breaks down and single tubes of various lengths and orientations are the result.

On the valve surface is a single central strutted process (CSP; fultoportula) associated with a central annulus (Fig. 8). This CSP normally has five satellite pores, although the range is 4–7 (Figs. 9, 10). The CSP may be separated from the annulus by an areola (Fig. 9). Occasionally a double annulus with two CSPs is seen (Fig. 11). Two labiate processes (LPs; rimoportulae) are present, separated on the valve margin by an angle of 140–170° (Fig. 14). In teratological forms up to four LPs can be found (Fig. 15), and in these the number of LPs may correspond to the number of annuli. The interior portion of the LP

may be perpendicular to the valve margin (Fig. 16) or diagonal (Fig. 17). The exterior of the LP is a long inflated tube (Fig. 18) in some cases, while in others (Fig. 12; see also Fryxell and Hasle 1972, Fig. 34; Hallegraeff, 1985, Fig. 25a) it is much shorter and not inflated.

Around the valve is a single row of marginal strutted processes (MSPs; Figs. 12–18, 23) that invariably have four satellite pores (Figs. 16, 17). At intervals of 4–8 MSPs the orientation of one MSP changes to nearly parallel to the pervalvar axis (Figs. 16–18, 23). This variation in MSP orientation is present in material from the Pacific Ocean (our samples; see also Fryxell and Hasle 1972, Fig. 34b) and Indian Ocean (Gerloff 1970, Fig. 25; Hallegraeff 1985, Fig. 25b) but has not been confirmed as present in Atlantic Ocean or Agulhas Bank material.

As has been noted before (Gerloff 1970; Round et al. 1990) the valvocopula is ornamented with regular rows of areolae. In our material the areolae are less regular, and the advalvar edge is ornamented with a series of irregular additional pores, sometimes lachrymiform (Fig. 18) and sometimes elongate slits. These are often obscured by the valve margin in entire cells, and their linear frequency varies from about 0.4–1.0 in comparison to the marginal strutted processes on the valve.

Cytology

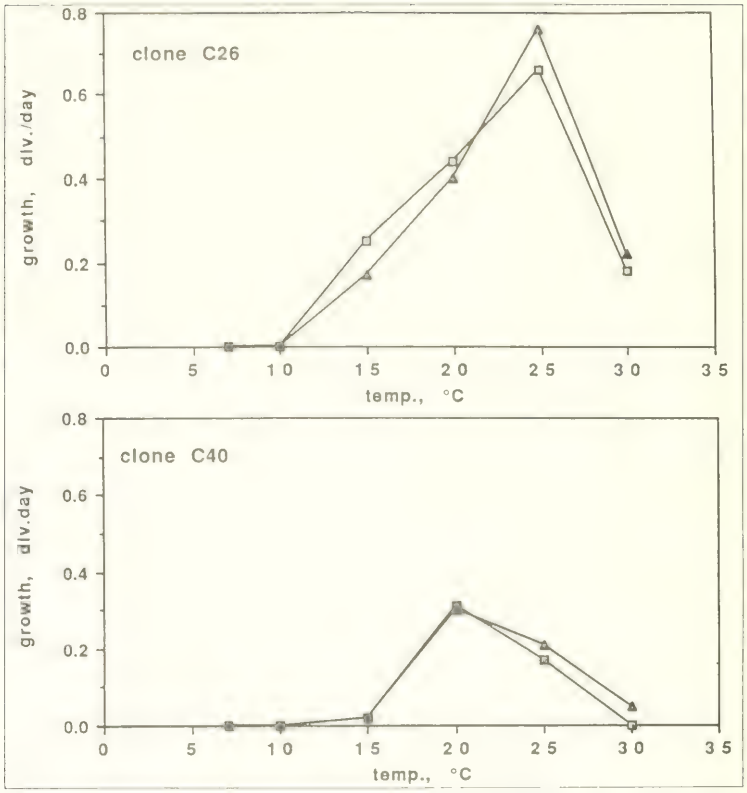
The association of the wing with the epitheca is clearly shown in Figures 19, 20, and 24. The upper part of the wing is anchored to the valvocopula, and the lower part is attached to the other epithecal bands. Wing material may extend over the valve surface to varying degrees (Fig. 24, arrowhead) to encompass the area of the MSPs. In several instances the MSPs contained organic material that may have some relationship to the wing (Figs. 21, 26), but no sections were seen that showed exact continuity of this material with the wing. Extruded material from the CSP was not seen, either in the epivalve (Fig. 20) or hypovalve (Figs. 19, 22).

Valvar plane sections (Fig. 25) and apical plane sections (Figs. 19, 22, 26) show high levels of Golgi formation associated with the nuclear envelope at different stages of the cell cycle (indicated by presence/absence of heterochromatin in the nucleus), as well as numerous irregularly oval chloroplasts with lenticular pyrenoids (Figs. 19, 22, 25). In cells with fully formed wings, the vacuole is mostly free of organic material (Figs. 19, 20, 24), whereas in cells in which the wing is not yet formed, the vacuole is filled with material exhibiting the same electron density as wing material (Fig. 22). These latter cells frequently are attractive to bacteria (Fig. 22), which is infrequently the case with winged cells. Dense vesicles (Schmid 1986) can be found near the valvocopula (Fig. 24) and more abundantly in cells in which electron dense material is accumulated internally (Fig. 22).

Growth in Culture

Two clones isolated from the same location were used in measurements of growth rate at a variety of temperatures and two light levels (Text Fig. 1). Both clones failed to grow at 10° C and above 30° C. Growth in clone C40 was negligible at 15° C, but substantial in clone C26. Clone C40 grew less well than clone C26 at all intermediate temperatures. The maximum growth rate for C40 was about 0.3 divisions per day, while C26 grew at a maximum rate of 0.7 divisions per day. In addition, the optimum temperature for C26 was 25° C, but C40 grew best at 20° C. Surprisingly, there were only minor differences between high and low light intensities in both clones.

Cells in culture provided additional observations in growth habit as well. In many cases, in both clones, *Planktoniella sol* assumed a colonial habit: up to 10 cells in chains joined



Text Figure 1. Growth rates of two *P. sol* clones at various temperatures and two light levels. Each data point is the mean of six calculations (open squares = high light; black triangles = low light).

by valvar contact were seen. Additionally, on rare occasions one or more threads (presumably chitin) were observed originating from the marginal strutted processes. Neither colonies nor chitin threads were seen in natural material.

Discussion

Planktoniella sol has been compared to *Thalassiosira eccentrica* in the past, because of the appearance of wingless *P. sol* cells (Gerloff 1970; Fryxell and Hasle 1972). In the light microscope, the most obvious differences, apart from the wing, are the paired labiate processes in *P. sol* and the presence of marginal spines and more numerous strutted processes in *T. eccentrica*. In the electron microscope, differences are seen in the satellite pores and orientation of strutted processes, and in the variability shown in teratological

TABLE 1. Morphological comparison of *P. sol* with *T. eccentrica*.

Cell feature	*Planktoniella sol*	*Thalassiosira eccentrica*
valve face	flat	flat
valve nargin	steep	rounded
valve mantle	less high than *T. eccentrica*	higher than *P. sol*
rows of areolae (teratological forms)	tangential (fasciculate)	tangential (fasciculate)
areolae cibra	pseudopores, coarser than *T. eccentrica*	pseudopores, more delicate than *P. sol*
areolae formina	with siliceous cilia or other fine structure	siliceous cilia reported only once
spines	lacking	marginal irregular ring
central strutted process (teratological forms)	1 (with 5 satellite pores) next to a central areola (= annulus) (1–3, with 4–7 satellite pores)	1 (with 4 sateliite pores) next to a central areola (= annulus) (1–2, with 3–5 satellite pores)
strutted processes on face valve	none	scattered
strutted processes at margin	1 ring (each SP with 4 satellite pores)	2 rings (each SP with 4 satellite pores)
orientation of marginal SPs	varies	regular, no alteration
chitin threads	rare	through all SPs
wing	marginal, circumferential	lacking
LPs at the margin (teratological forms)	2 1–4 LPs according to number of annuli; LPs always at margin	1 1–3 (4) according to number of annuli; LPs move to face valve along fusion lines
valvocopula (VC)	with slits and pores at valve junction site	with regular pores; more rigid than *P. sol*
girdle bands	? 2–4 per theca	5+ per theca

processes in *P. sol* and the presence of marginal spines and more numerous strutted processes in *T. eccentrica*. In the electron microscope, differences are seen in the satellite pores and orientation of strutted processes, and in the variability shown in teratological forms. These are all summarized in Table 1 (data on *T. eccentrica* from Fryxell and Hasle 1975; Schmid and Schulz 1979; Schmid 1984a, b; Fryxell et al. 1981; Rivera 1981). Apart from the presence of the wing, all the variation in *P. sol* falls within the range of structures seen in the many species of *Thalassiosira*. But as Round (1972) has pointed

forms. These are all summarized in Table 1 (data on *T. eccentrica* from Fryxell and Hasle 1975; Schmid and Schulz 1979; Schmid 1984a, b; Fryxell et al. 1981; Rivera 1981). Apart from the presence of the wing, all the variation in *P. sol* falls within the range of structures seen in the many species of *Thalassiosira*. But as Round (1972) has pointed out, the presence of a wing is sufficient to distinguish between the two genera. *Planktoniella sol* shares the features of an eccentric areolar pattern and two labiate processes per valve, with *T. elsayedii* Fryx. (Fryxell 1975), and overlaps considerably in valve diameter and strutted process arrangement. However, *P. sol* usually has coarser areolae, and always lacks the marginal spines that are a constant feature of *T. elsayedii*.

There has been considerable interest in how *P. sol* makes its wing. The clones used in this study died before complete examination of cytological events at different, defined stages of the cell cycle were completed. Nevertheless, some of the possible mechanisms for wing formation can be examined.

(1) Wing chambers are formed by extrusion of material through MSPs (fultoportulae), with pervalvar-oriented MSPs responsible for individual wing chamber walls. We find this unlikely, since: (a) the spacing of pervalvar-oriented MSPs is quite irregular compared to the spacing of wing chambers; and, (b) the lack of early developmental stages of the wing in the many sections examined suggests that wing formation is a fairly time-constrained process, and the extrusion of such a large amount of material in a short time through the MSPs seems infeasible. However, we cannot preclude the possibility of these pervalvar-oriented MSPs having a function in valve formation where they may play a similar role to that of tricornate spines in *T. eccentrica*, in that they are molded by mutual cytoplasmic adhesions of the sibling cells (Schmid 1984a, b). Whatever its morphological and functional significance, the altered orientation must be "programmed" very early in valve morphogenesis, i.e., during base layer formation. Such a process pattern does not occur in *P. muriformis* (Round et al. 1990, and PEH, pers. obs.) or, to our knowledge, in any other diatom with strutted processes.

(2) Each MSP forms a single wing chamber. In a number of cells from Baja California the number of wing chambers and MSPs are about the same. Moreover, some MSPs contain organic material (Figs. 21, 26) and the wing can extend over the valve to the area of the MSPs (Fig. 24). However, in Agulhas Bank material, in a few cells examined from the Caribbean Sea, and from measurements (where possible) of published SEM photos (Gerloff 1970; Fryxell and Hasle 1972; Hallegraeff 1985; Round et al. 1990), the ratio of wing chambers to MSPs departs significantly from unity. Organic material extruded into the MSPs has a different appearance from wing material either in place or what could be wing precursor material in internal lysosomal vesicles; it is hardly distinguishable from labiate process mucopolysaccharide reported by Medlin et al. (1980). It also appears different from the β–chitin fibers that are produced by SPs in other centric genera (Herth 1979). Therefore, we believe it is unlikely that wing formation is a function of the marginal strutted processes.

(3) Wing chambers are extruded through pores and slits in the valvocopula. The upper portion of the wing is firmly attached to the valvocopula (Figs. 19, 20, 24), and the size and spacing of the pores and slits are less regular than the MSPs, which is also the case with wing chambers. These pores are quite difficult to see unless the valvocopula is separated from the valve. Coincidence of physical proximity and spacing suggest that these pores and slits might be the locus for wing extrusion. Unresolved questions remain. Dense vesicles, originating in the Golgi bodies and having a significant role in termination of the silicification process and production of the cell's outer organic layer (Schmid 1986, 1988), are present near the upper and lower junctures of the valvocopula (Figs. 24–26).

Their presence near the site of wing extrusion in non-cytokinetic cells raises the question of a possible role in wing formation; they appear to be more abundant in cells containing significant electron dense material internally (Fig. 22). Another problem is the lack of TEM observations through all cytokinetic stages. Presumably the wing is formed after division and silicification of new valves is complete. As yet we have too few sections to define the details of the wing extrusion sequence, particularly transport of wing material to the exterior of the cell. The degeneration of the wing into a series of single chamber tubes when treated with APM suggests an involvement of microtubule activity. Microtubules may mediate the transport and orientation of vesicles delivering material for wing chamber tubes as they are extruded, and hydration of the organic material may cement them into a coherent wing. When microtubule function is inhibited, single chamber tubes result. These problems will be addressed when *P. sol* is re-established into culture.

Our results with the anti-microtubular herbicide APM confirms Karsten's (1928:147) earlier suggestion that the wing is composed of single tubes that fuse laterally. The contact zones of the tubes constitute the darker staining rays (Figs. 3–6). The mechanics of single tube formation with APM are not understood. Other microtubule inhibitors such as colchicine induce morphological and cytochemical changes of the Golgi (Pavelka and Ellinger 1981, 1983). APM also interferes with calcium metabolism (Hertel et al. 1980); both pathways could influence production and transport of Golgi-derived metabolites, leading to a potential loss of "stickiness" at tubal contact zones, apart from a possible tubal orientation role for microtubules. It is interesting that, in *T. eccentrica* (Schmid 1984b), APM inhibits chitin thread formation (thus also colony formation). Both phenomena could be based on the same inhibition mechanism.

In common with many other diatoms, clonal variation in growth rate and temperature optimum is evident in culture. Smayda (1958), based on distribution records, found a mean temperature of 19.2° C, and suggested that occurrences below 10–15° C represented "sterile distributions." Our data suggest this view is correct. *Planktoniella sol* is usually characterized as a tropical species. Its frequent occurrence, and its ability to grow, at temperatures < 20° C seem to argue against its classification as a strictly tropical species; indeed, clone C40 had its maximum growth rate at 20° C, and both clones showed some growth at 15° C. The oceanic nature of the species is seen in its distribution records at salinities of 33.76–39.15 ‰ (Smayda 1958); clones C26 and C40 were isolated from waters with a salinity range of 33.6–34.2 ‰ (Smayda 1975). As with most phytoplankton, direct extrapolation of natural occurrences to results obtained under stressful (for the organism) laboratory conditions must be interpreted with some circumspection. Nevertheless, the variations in growth rate in two clones from the same location, and the minor differences in morphology from geographically separate areas (also seen in the companion species *P. muriformis*; Round 1972:228 and pers. obs.) imply that morphological and physiological "races" of *P. sol* exist.

Conclusions

(1) Wing formation appears to be a result of extrusion through the valvocopula of the epitheca, with anchoring points on the epivalve, valvocopula, and epitheca bands. The participation of marginal strutted processes in wing formation is unlikely.

(2) Wing material may be synthesized in vesicles formed from the Golgi bodies, with possible involvement of the dense vesicles and microtubules.

(3) Temperature dependent clonal variation in growth rate is demonstrated; the temperature range for growth in culture is similar to that of occurrences in nature.

(4) Under culture conditions, *Planktoniella sol* forms colonies joined at the valves, and is capable of producing chitin-like threads, in common with other members of the Thalassiosiraceae.

(5) Details of the sequence of events leading to wing extrusion will depend on examination of all stages of the cell cycle.

Acknowledgements

Portions of this work were supported by NSF/OCE-8309383 to PEH and the Austrian FFWF (P-Bio-2787) to AMS. AMS thanks J. Jordan for a clone of *P. sol*. Since the writing of this, *P. sol* has been discussed in relation to other diatoms by Hallegraeff (Diat. Res. 7:15–23; 1992) and Hasle and Syvertsen (Nova Hedw. Beih. 106:297–314; 1993).

Literature Cited

CUPP, E. E. 1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Oceanogr. 5:1–238.

FRYXELL, G. A. 1975. Three new species of *Thalassiosira*, with observations on the occluded process, a newly observed structure of diatom valves. Nova Hedwigia, Beih. 53:57–75.

FRYXELL, G. A. AND G. R. HASLE. 1972. *Thalassiosira eccentrica* (Ehrenberg) Cleve, *T. symmetrica* sp. nov. and some related centric diatoms. J. Phycol. 8:297–317.

FRYXELL, G. A., G. F. HUBBARD, AND T. A. VILLAREAL. 1981. The genus *Thalassiosira*: variations of the cingulum. Bacillaria 4:41–63.

GERLOFF, J. 1970. Elektronmikroskopische Untersuchungen an Diatomeenschalen VII. Der Bau der Schale von *Planktoniella sol* (Wallich) Schütt. Nova Hedwigia, Beih. 31:203–234.

GUILLARD, R. R. L. 1973. Division rates. Pp. 289–311 *in* Handbook of Phycological Methods: Culture Methods and Growth Measurements, J. R. Stein, ed. Cambridge University Press, London.

———. 1975. Culture of phytoplankton for feeding marine invertebrates. Pp. 29–60 *in* Culture of Marine Invertebrate Animals, W. L. Smith and M. H. Chanley, eds. Plenum Publishing Corp, New York.

HALLEGRAEFF, G. M. 1985. Species of the diatom genus *Thalassiosira* in Australian waters. Bot. Mar. 27:495–513.

HERTEL, C., H. QUADER, D. G. ROBINSON, AND D. MARM. 1980. Anti-microtubular herbicides and fungicides affect Ca^{2+} transport in plant mitochondria. Planta 149:336–340.

HERTH, W. 1979. The site of β-chitin fibril formation in centric diatoms. II. The chitin-forming cytoplasmic structures. J. Ultrastr. Res. 68:16–27.

KARSTEN, G. 1928. Abteilung Bacillariophyta (Diatomeae). Pp. 105–303 *in* Die Naturlichen Pflanzenfamilien, Vol. 2, 2nd edition, A. Engler and K. Prantl, eds. Wilhelm Englemann, Leipzig.

MEDLIN, L. K., R. M. CRAWFORD, AND R. A. ANDERSEN. 1986. Histochemical and ultrastructural evidence for the function of the labiate process in the movement of centric diatoms. Br. Phycol. J. 21:297–301.

PAVELKA, M. AND A. ELLINGER. 1981. Effect of colchicine on the Golgi apparatus of rat jejunal absorptive cells. Ultrastructural localization of thiamine pyrophosphatase and acid phosphatase activity. Europ. J. Cell Biol. 24:53–61.

———. 1983. Effect of colchicine on the Golgi complex of rat pancreatic acinar cells. J. Cell Biol. 97:737–748.

RIVERA, P. 1981. Beiträge zur Taxonomie und Verbreitung der Gattung *Thalassiosira* Cleve (Bacillariophyceae) in den küstengewässern Chiles. Bibl. Phycologia 56:1–120.

ROUND, F. E. 1972. Some observations on colonies and ultrastructure of the frustule of *Coenobiodiscus muriformis* and its transfer to *Planktoniella*. J. Phycol. 8:222–231.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms. Cambridge University Press, Cambridge.

SCHMID, A. M. 1984a. Tricornate spines in *Thalassiosira eccentrica* as a result of valve modelling. Pp. 71–95 *in* Proceedings of the Seventh Symposium on Recent and Fossil Diatoms, D. G. Mann, ed. O. Koeltz, Koeningstein.

———. 1984b. Wall morphogenesis in *Thalassiosira eccentrica*: comparison of auxospore formation and the effect of MT-inhibitors. Pp. 47–70 *in* Proceedings of the Seventh Symposium on Recent and Fossil Diatoms, D. G. Mann, ed. O. Koeltz, Koenigstein.

———. 1986. Wall morphogenesis in *Coscinodiscus wailesii* Gran et Angst II. Cytoplasmic events of valve morphogenesis. Pp. 293–314 *in* Proceedings of the Eighth Symposium on Recent and Fossil Diatoms, M. Ricard, ed. O. Koeltz, Koenigstein.

———. 1988. The special Golgi-ER-mitochondrium unit in the diatom genus *Coscinodiscus*. Plant Syst. Evol. 158:211–223.

SCHMID, A. M. AND D. SCHULZ. 1979. Wall morphogenesis in diatoms: deposition of silica by cytoplasmic vesicles. Protoplasma 100:267–288.

SMAYDA, T. J. 1958. Biogeographical studies of marine phytoplankton. Oikos 9:158–191.

———. 1975. Net phytoplankton and the greater than 20-micron phytoplankton size fraction in upwelling waters off Baja California. Fish. Bull. 73:38–50.

VAN LANDINGHAM, S. L. 1978. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Part VI. *Neidium* through *Rhoicosigma*. J. Cramer Verlag, Vaduz.

Explanation of Plates

Plate 1, Figures 1–6

FIGURE 1. Normal cell: areolae in tangential rows, one central strutted process (fultoportula), two marginal labiate processes (rimoportulae); marginal strutted processes not visible in LM; wing composed of 52 tubular segments. FIGURE 2. Wing deformation in culture with normal valve. FIGURES 3, 4. Wing deformation in culture with normal valves: wing segments as single tubes at different levels of focus. FIGURE 5. Treatment with 10^{-4} % APM: wing with single tubes and aberrant valve patterns. FIGURE 6. Treatment with 10^{-4} % APM: detail of wing segments and aberrant valve. (Figs. 1–5, × 875; Fig. 6, × 200).

Plate 2, Figures 7–18

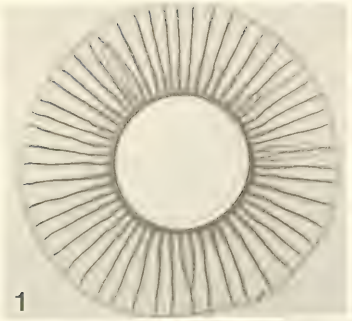
FIGURE 7. Edge of wing, thickness ca. 7 µm (LM, × 550). FIGURE 8. Valve interior: annulus and adjacent central strutted process with five satellite pores (SEM, × 6000). FIGURE 9. Valve interior: one areola separates annulus from central strutted process with four satellite pores (SEM, × 6000). FIGURE 10. Central strutted process with seven satellite pores (SEM, × 12,000). FIGURE 11. Double annulus and two central strutted processes with four and five satellite pores (SEM, × 6000). FIGURE 12. Entire cell, wing with thickened margins; one labiate process visible. Valve diameter 28 µm, total diameter 88 µm (SEM, × 1300). FIGURE 13. Valve exterior: areolae in tangential rows, two labiate processes separated by ca. 160° (arrowheads) (SEM, × 950). FIGURE 14. Valve interior: single central strutted process, two labiate processes separated by ca. 160° (arrowheads) (SEM, × 950). FIGURE 15. Valve interior with three labiate processes (arrowheads) (SEM, × 950). FIGURE 16. Valve interior margin: labiate process perpendicular to valve margin; one marginal strutted process closer to pervalvar axis (arrowhead) (SEM, × 6000). FIGURE 17. Valve interior margin: labiate process diagonal to valve margin; one marginal strutted process (on the left) oriented closer to pervalvar axis (SEM, × 6000). FIGURE 18. Valve exterior margin: inflated exterior portion of labiate process; one marginal strutted process (at top) closer to pervalvar axis; irregularly shaped valvocopula pores at margin (SEM, × 6000).

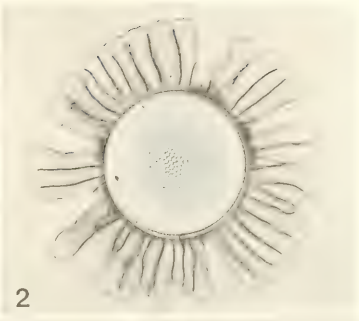
Plate 3, Figures 19–22

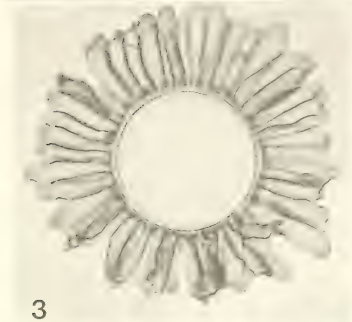
FIGURE 19. Apical plane section: multiple chloroplasts with lenticular pyrenoids; vacuole electron translucent; central strutted process in hypovalve; wing anchored on epicingulum bands (TEM, × 6000). FIGURE 20. Glancing apical plane section: wing attached to epicingulum; vacuole electron translucent; central strutted process in the epivalve (TEM, × 3500). FIGURE 21. Extrusion of organic material through a marginal strutted process (TEM, × 19,000). FIGURE 22. Apical plane section, prior to wing formation: vacuole filled with electron dense material; pyrenoids much reduced; bacteria congregating at areolae and at junctures of bands; several dense vesicles and intermediate-sized Golgi vesicles are present. The central strutted process of the hypovalve is marginally sectioned (TEM, × 8000).

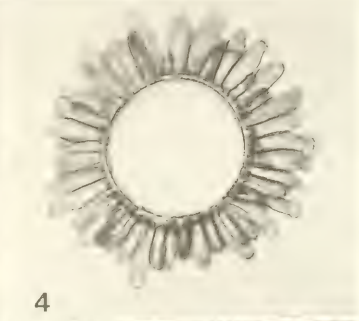
Plate 4, Figures 23–26

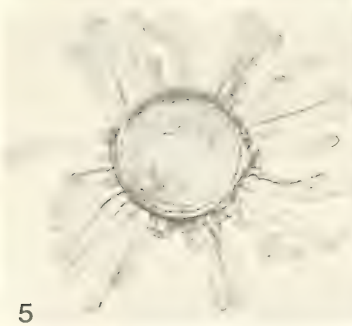
FIGURE 23. Internal margin of valve: marginal strutted processes with four satellite pores; three marginal strutted processes (arrowheads) oriented closer to the pervalvar axis (SEM, × 6000). FIGURE 24. Apical plane section, detail of FIGURE 19: upper surface of the wing is anchored at the upper and lower margin of the valvocopula, and extends over the valve margin (arrowhead) to the area of the marginal strutted processes. The lower surface of the wing is anchored to the second copula of the epitheca. A dense vesicle is seen near the junction of the valvocopula and copula (arrow) (TEM, × 14,000). FIGURE 25. Valvar plane section through girdle band region: lack of heterochromatin in the nucleus suggests an interphase cell; intense production of Golgi material around nuclear envelope; dense vesicles abundant; wing not visible, but fibrillar material in vacuoles is abundant (TEM, × 10,000). FIGURE 26. Detail of oblique apical plane section: active production of small vacuoles with electron dense material originating from perinuclear Golgi bodies; dense vesicle (white arrow) at inner valve surface; marginal strutted processes with material being extruded (TEM, × 24,000).

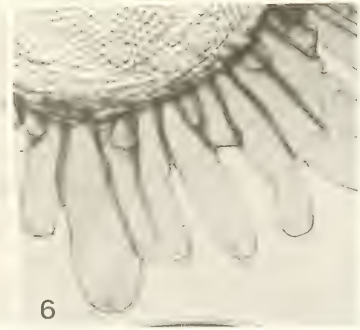

1

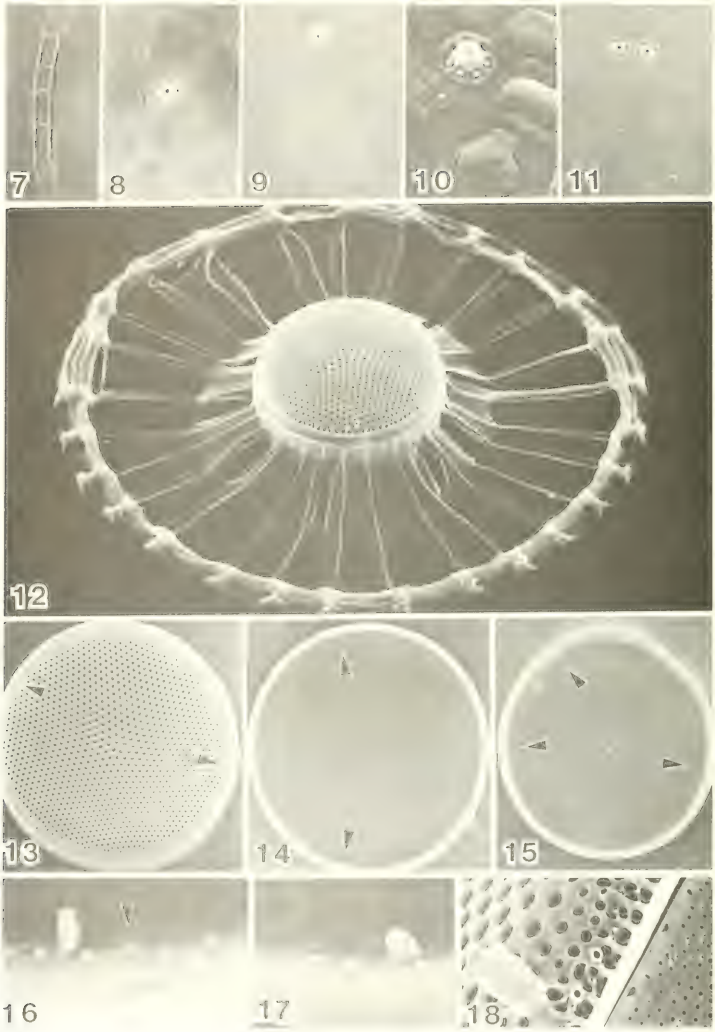

2


3

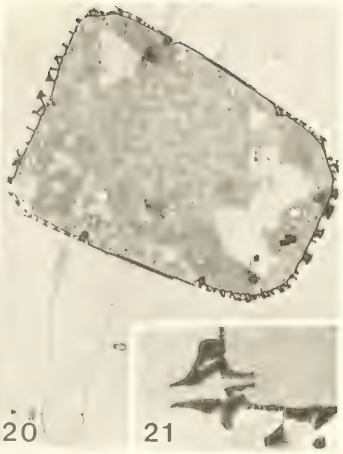

4

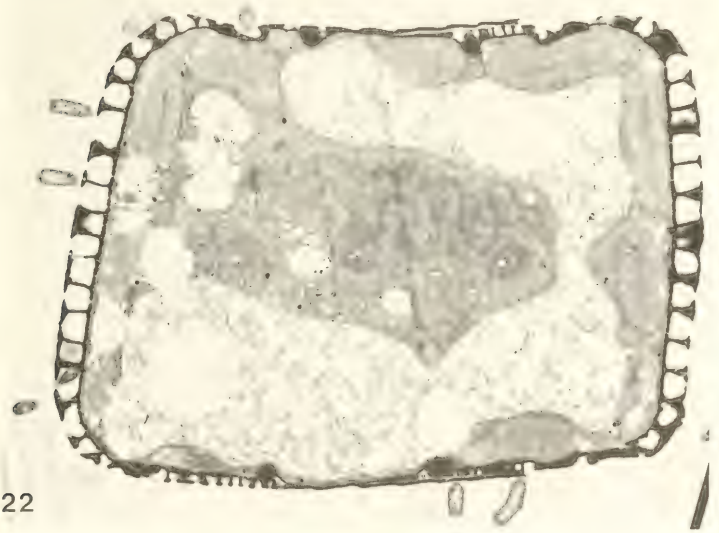

5


6


7
8
9
10
11
12
13
14
15
16
17
18

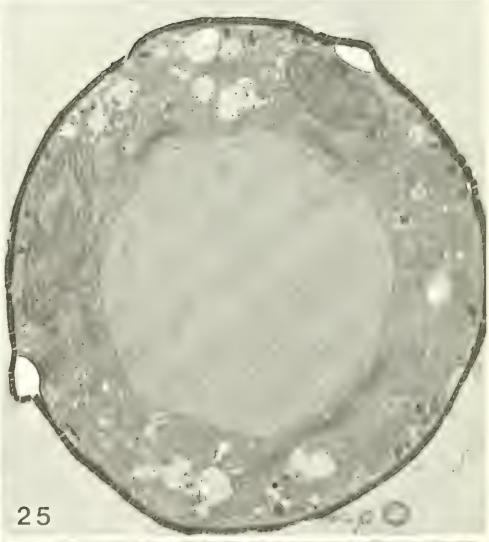
19

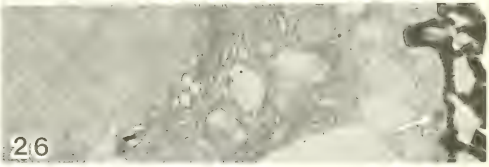

20 21


22

23

24


25


26

Cytoplasmic Fine Structure of Two *Encyonema* Species

by

John P. Kociolek

Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

and

Linda Sicko-Goad and Eugene F. Stoermer

Center for Great Lakes and Aquatic Sciences, University of Michigan, 2200 Bonisteel Boulevard, Ann Arbor, Michigan 48109-2099

with 4 plates

Abstract: Cytoplasmic fine structure and growth habit of *Encyonema caespitosum* and *E. minutum* are described. *E. caespitosum* grows in mucilaginous tubes while *E. minutum* is an epiphyte, its cells encapsulated in mucilage. Both species have the closed portion of the C-shaped chloroplast and the pyrenoid positioned near the ventral valve margin and the nucleus positioned near the dorsal margin. The diatotepic layer is fused with the axial rib of the raphe and subtends or protrudes into puncta of the valve face and mantle. Five vesicle types are observed in *E. caespitosum* and four of these types are also found in *E. minutum*. Vesicles appear to be related to mucilage production, and differences in the growth habits of these two species may be related to vesicle type. *Encyonema caespitosum* has vesicles that contain a dense fibrillar-like material that may impart rigidity to the tubes, while *E. minutum* lacks such vesicles and forms only an amorphous covering. An understanding of the relationship of growth habit to cytoplasmic fine structure in other freshwater cymbelloid and gomphonemoid diatoms may provide information on interrelationships within this lineage.

Introduction

Intracellular components of a broad range of diatom taxa have been described using transmission electron microscopy (e.g., Drum et al. 1966). However, comparisons between closely related taxa are rare. Freshwater cymbelloid and gomphonemoid diatoms appear to represent a natural evolutionary lineage. Members of this clade have been grouped together, classically, on the basis of valve asymmetry; cymbelloid diatoms being asymmetrical about the apical axis, gomphonemoid diatoms being asymmetrical about the transapical axis (Müller 1905; Hustedt 1930). Kociolek and Stoermer (1988) identified a suite of cytological and valve features that define this clade, including the type of sexual

reproduction, relative position of the chloroplast, pyrenoid and nucleus, deflection of the distal raphe ends, and presence of apical pore fields. Members of this lineage secrete mucilage to produce various types of growth forms, including stalks, tubes, and encapsulated cells. The purpose of this work is to describe and compare cytoplasmic fine structure of closely related taxa relative to mucilage secretion. This approach may help us identify additional characters useful in resolving interrelationships. In this paper we examine the fine structure of two *Encyonema* species, *E. caespitosum* Kützing and *E. minutum* (Hilse *ex* Rabh.) D. G. Mann in Round et al.

Materials and Methods

Specimens were collected from rocks along the shore of Lake Superior in Marquette, Michigan, on 20 October 1988. Collections were initially split into two parts; one portion was field-fixed in 1% paraformaldehyde-gluteraldehyde following the procedure described by Lazinsky and Sicko-Goad (1979) and the other was retained as a live sample. All samples were kept on ice and returned to the lab for processing.

Live samples were processed for light (LM) and scanning electron microscopy (SEM). Material was boiled in nitric acid and processed according to the protocol described in Patrick and Reimer (1966). Cleaned material was repeatedly rinsed with distilled water and settled to remove acid and oxidation by-products, then air-dried onto coverglasses. For LM, coverglasses containing dried material were mounted onto slides with Hyrax and viewed with either a Leitz Ortholux or Dialux-20 microscope.

A portion of fixed material was washed in phosphate buffer (pH 7.2), then stained with 0.5% Methylene Blue for approximately 1 minute. Light microscopic observations were made on stained material. For TEM, field-fixed samples were postfixed in 1% osmium tetroxide in 0.05M sodium cacodylate buffer (pH 7.2) for 1 hour. Samples were then dehydrated in a graded ethanol-propylene oxide series and embedded in epoxy resin. Thin sections were cut with a diamond knife, collected on cleaned, formvar-coated copper grids, and stained with aqueous uranyl acetate (Watson 1958). Sections were examined in a Philips 400 TEM operating at 80 kV.

Results

Growth Habit and Valve Morphology

Valves of Lake Superior specimens of *E. caespitosum* (Fig. 1) are 22–37 µm long and 10–12 µm broad and have 9–12 striae in 10 µm. The dorsal margin is strongly arched and the ventral margin is straight or slightly tumid. The ends are slightly protracted. Specimens of *E. caespitosum* were found residing in tubes (Figs. 2–4). Cells were packed at the tips of tubes (Fig. 2), but were more widely spaced in other sections (Figs. 3, 4). Tube walls were usually smooth, but protrusions or bumps also occurred (Figs. 5, 6). Cells were connected by mucilaginous strands within tubes (Fig. 4).

Valves of *E. minutum* found in Lake Superior are small (8.5–19 µm long, 3–6 µm broad) and have 14–16 striae in 10 µm (Fig. 8). Cells were epiphytic on various substrates, occurring individually or in small clusters. Most cells were encapsulated in mucilage and oriented with their ventral margins parallel to the substrate (Figs. 9, 10).

Cytoplasmic Fine Structure

In both *E. caespitosum* and *E. minutum* the nucleus is positioned toward the dorsal margin and surrounded by an extensive Golgi-ER network (e.g., Fig. 7). The pyramidially shaped pyrenoid is located near the ventral valve margin. Vacuoles surrounded by peripheral

cytoplasm containing chloroplast profiles are placed on both sides of the central cytoplasmic bridge.

In transverse section marginal to the central cytoplasmic bridge both species have a single C-shaped chloroplast that occupies a large portion of the intracellular space (Figs. 11, 13). The closed portion of the "C" is positioned along the ventral valve margin. The narrow, pointed end of the pyrenoid projects toward the cell interior. The pyrenoid is bisected by "double disc bands" (*sensu* Drum and Pankratz 1964) of chloroplast lamellae. Mitochondria, with tubular cristae, are distributed near the periphery of the cytoplasm adjacent to the frustule and in the central cytoplasmic bridge (Figs. 11–13).

Five types of vesicles have been identified in *E. caespitosum*, four of which are also found in *E. minutum*. The first four types described are contained within the plasmalemma and include:

(1) Small vesicles of fairly uniform density that are found primarily about the central portion of the cytoplasm in the vicinity of Golgi (V1) (Figs. 12, 14).

(2) Small vesicles containing fibrillar material, which is uniform in density throughout the vesicle (V2). These are found throughout the cytoplasm (Figs. 15, 22).

(3) Large vesicles containing fibrillar material that are somewhat condensed in the center and have thin strands radiating peripherally (V3) (Figs. 16, 22).

(4) Large vesicles with densely staining centers of fibrillar material and radiating strands (V4) (Figs. 16, 17). This type of vesicle is lacking in *E. minutum*. Both types of fibril-containing vesicles are found throughout the cytoplasm and also can be found fused with the plasmalemma.

A fifth vesicle type (V5) is observed between the plasmalemma and a dense-staining layer that appears to be the diatotepum (sensu von Stosch 1981). The area between the plasmalemma and diatotepum has been referred to as the "subfrustular zone" by Drum and Pankratz (1964). Vesicles within this zone are small, with dark outlines and undifferentiated, less dense interiors (Figs. 17, 23).

The diatotepic layer beneath the valve face of both *Encyonema* species may project into the puncta, while along the valve margin and mantle it merely subtends the valve (Figs. 7, 11, 13, 24). Thickenings of the diatotepum are associated with interior valve ribs in the valve margin and mantle region. The diatotepic layer appears to fuse with the axial rib of the raphe system. Fine strands of a density similar to fibrils comprising the tube occur external to the diatotepic layer but within the puncta (Figs. 17–19). Just interior to the raphe, V2-, V3-, and V4-type vesicles (in *E. caespitosum* only), endoplasmic reticula, and mitochondria are present (e.g., Fig. 19). In this region V5-type vesicles are observable external to the plasmalemma. Fibrillar material is found through and outside of the raphe slit, and this material resembles exudate from the puncta (Figs. 18, 19).

TEM observations on the mucilaginous tubes of *E. caespitosum* indicate mucilage is in two (rarely three) layers; a narrow, dense outer layer and a wide, less dense, inner layer (Fig. 21). In some sections a region of intermediate density is observable. The margin of the outer layer is crenulate to broadly lobed. Mucilage of both layers is fibrillar in appearance. Despite the typical appearance in the light microscope of a large amount of unoccupied space within tubes, cells and wall material occupy most of the tubes' diameter. The mucilaginous material that encapsulates *E. minutum* is uniform in structure and appearance and less dense (Fig. 24) relative to the structure of tubes seen in *E. caespitosum*.

Discussion

Cellular fine structure of *E. caespitosum* and *E. minutum* resembles that of other diatoms, particularly other members of the freshwater cymbelloid and gomphonemoid lineage. Similarities to other diatoms in this lineage exist with regard to the structure of the chloroplast, Golgi, endoplasmic reticulum (Dawson 1973), and membrane-bound pyrenoid with bisecting lamellae (e.g., Drum and Pankratz 1964; Stoermer et al. 1964; Drum et al. 1966; Daniel et al. 1980). The diatotepum is also reported for a broad range of diatoms (centric, araphid, and raphid) (von Stosch 1977, 1981, and references therein). This structure has been identified by Drum and Pankratz (1964) in specimens of *Gomphonema parvulum* Kütz., although no such structure was demonstrated by Dawson (1973) for this same species. Von Stosch (1981) indicates the presence of poroids in the diatotepic layer at sites of mucilage secretion in *Odentella aurita* Ag. and *Bellerochea polymorpha* Hargraves & Guillard. No poroids were observed through this layer in *E. caespitosum* or *E. minutum* although mucilage secretion occurs along its entirety. Despite the lack of observable poroids in the two *Encyonema* species, presence of rounded vesicles on the interior of the diatotepic layer and fine strands or fibrils on their exterior suggest some physical transfer occurs across the layer, perhaps through some as yet undemonstrable openings. Siliceous, perforated internal coverings of the puncta (termed ricae *sensu* Ross et al. 1979) have been observed by Mayama and Kobayasi (1986) in *Navicula mobiliensis* var. *minor* Patr. and *N. goeppertiana* (Bleisch) H. L. Smith. Their schematic representations of this structure resemble both the position and structure of the diatotepic layer. The diatotepum of the *Encyonema* species stains to almost the same degree as siliceous valve components. Thus, the suggested organic nature of the diatotepum (von Stosch 1977, 1981), and its relationship to the ricae of pennates and vela of centric diatoms may be in need of reevaluation.

The process of mucilage secretion in *E. caespitosum* and *E. minutum*, as suggested by the position of vesicles within the cells, resembles, in general, models proposed by Borowitzka and Volcani (1978) for organic cell wall formation in *Phaeodactylum tricornutum* Bohlin and by Edgar and Pickett-Heaps (1984) for movements in raphid diatoms. In both models material deposited across outer membranes produces elongated fibrils externally. In the two *Encyonema* species fibrillar vesicles appear to fuse with, and release material across, the plasmalemma. This material enters the zone between the plasmalemma and diatotepic layer, then is released across the diatotepic layer to the exterior. The material then appears as elongated fibrils. A similar process occurs at the raphe slit. Due to the apparent fusion of the diatotepic layer with the axial rib no subfrustular zone exists and thus vesicles are deposited directly into the raphe slit. Drum and Pankratz (1964) show mucilage exudation from the raphe of *G. parvulum*, however no fibrillar vesicles are evident. There is an inverse relationship between the number of V4-type vesicles and volume of tube material in *E. caespitosum*, suggesting these vesicles play a role in tube formation. In cells surrounded by a large amount of tube material, additional tube production is minimal and vesicle numbers are low. In cells surrounded by little or no tube material (at forming tips or isolated outside tubes), tube production is accomplished through increased numbers of vesicles. Although numerous authors have reported fibril-like material in vesicles of diatoms (Drum and Pankratz 1964; Stoermer et al. 1965; Taylor 1972; Gibson 1979; Walker et al. 1979; Edgar 1980; Edgar and Pickett-Heaps 1984; Sicko-Goad 1986; Gordon 1987), the vesicles found in *E. caespitosum* most closely resemble those described in *Amphora* species. Vesicles with dark staining margins located outside the plasmalemma but within the cell (no diatotepum was documented), as well as fibrillar vesicles were observed in *A. veneta* (Daniel et al. 1980). Differences between *E. minutum* and *E. caespitosum* exist with regard to growth habit and lack of dense

fibrillar vesicle (called V4 vesicle here) in *E. minutum*. These differences may be related. The mucilaginous tubes of *E. caespitosum* are well defined and comprised of 2–3 distinct layers of fibrillar material. Mucilage encapsulating cells of *E. minutum* is uniform in structure, resembling a thick organic "skin" or casing as seen in other diatoms (e.g. Rosowski et al. 1983, 1986). The V4 type vesicles found in *E. caespitosum* may help impart rigidity to the tubes and help account for growth habit differences. Examination of other taxa in the cymbelloid and gomphonemoid lineage, and their close allies, may help determine if vesicle differences are reflective of growth form type and/or pattern of evolutionary descent.

Acknowledgements

Research funded by Grant BSR-8722516 of the National Science Foundation.

Literature Cited

BOROWITZKA, M. A. AND B. E. VOLCANI. 1978. The polymorphic diatom *Phaeo-dactylum tricornutum*: ultrastructure of its morphotypes. J. Phycol. 14:10–21.

DANIEL, G. F., A. H. L. CHAMBERLAIN, AND E. B. G. JONES. 1980. Ultrastructural observations on the marine fouling diatom *Amphora*. Helgoländer Meeresunters. 34:123–149.

DAWSON, P. A. 1973. Observations on the structure of some forms of *Gomphonema parvulum* Kütz. II. The internal organization. J. Phycol. 9:165–175.

DRUM, R. W. AND H. S. PANKRATZ. 1964. Pyrenoids, raphes and other fine structure in diatoms. Amer. J. Bot. 51:405–418.

DRUM, R., H. S. PANKRATZ, AND E. F. STOERMER. 1966. Electron microscopy of diatom cells. In Diatomeenschalen im elektronenmikroskopischen Bild. Teil VI. J-G. Helmcke and W. Krieger, eds. J. Cramer, Lehre.

EDGAR, L. A. 1980. Fine structure of *Caloneis amphisbaena* (Bacillariophyta). J. Phycol. 16:62–72.

EDGAR, L. A. AND J. D. PICKETT-HEAPS. 1984. Diatom locomotion. Prog. Phycol. Res. 3:47–88.

GIBSON, R. A. 1979. Observations of stalk production by *Pseudohimantidium pacificum* Hust. & Krasske (Bacillariophyceae: Protoraphidaceae). Nova Hedwigia 31:899–915.

GORDON, R. 1987. A relatiatory role for algal projectiles, with implications for the mechanochemistry of diatom gliding motility. J. Theor. Biol. 127:418–436.

HUSTEDT, F. 1930. Bacillariophyta (Diatomeae). In Die Süsswasser-Flora Mitteleuropas, Heft 10. A. Pascher, ed. Gustav Fisher, Jena.

KOCIOLEK, J. P. AND E. F. STOERMER. 1988. A preliminary investigation of the phylogenetic relationships among the freshwater, apical pore field-bearing cymbelloid and gomphonemoid diatoms (Bacillariophyceae). J. Phycol. 24:377–385.

LAZINSKY, D. AND L. SICKO-GOAD. 1979. Paraformaldehyde-gluteraldehyde as a routine phytoplankton fixative. Micron 10:49–50.

MAYAMA, S. AND H. KOBAYASI. 1986. Observations of *Navicula mobiliensis* var. *minor* Patr. and *N. goeppertiana* (Bleisch) H. L. Smith. Pp. 173–182 *in* Proceedings of the 8th Symposium on Living and Fossil Diatoms, M. Ricard, ed. O. Koeltz, Keonigstein.

MÜLLER, O. 1905. Bacillariaceen aus dem Nyassland und einigen benachbarten Gebieten. III. Naviculoideae, Gomphonemineae, Nitschioideae. Engler's bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr. 36:137–206.

PATRICK, R. M. AND C. W. REIMER. 1966. The Diatoms of the United States. Vol. I. Acad. Nat Sci. Philadelphia, Monograph No. 13, 688 pp.

ROSOWSKI, J. R., K. D. HOAGLAND, AND S. C. ROEMER. 1983. Valve and band morphology of some freshwater diatoms. IV. Outer surface mucilage of *Navicula confervacea* var. *confervacea*. J. Phycol. 19:342–347.

ROSOWSKI, J. R., S. C. ROMER, J. PALMER, AND K. D. HOAGLAND. 1986. Extracellular association and adaptive significance of the bas-relief mucilage pad of *Achnanthes lanceolata* (Bacillariophyta). Diatom Res. 1:113–129.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

SICKO-GOAD, L. 1986. Rejuvenation of *Melosira granulata* (Bacillariophyceae) from the anoxic sediments of Douglas Lake, Michigan. II. Electron microscopy. J. Phycol. 22:28–35.

SICKO-GOAD, L., J. P. KOCIOLEK, AND E. F. STOERMER. 1989. Patterns of mucilage production and secretion in pennate diatoms. Pp. 1016–1017 *in* Proceedings of the 47th Annual Meeting of the Elctron Microscopy Society of America, G. W. Bailey, ed. San Francisco Press, San Francisco.

STOERMER, E. F., H. S. PANKRATZ, AND C. C. BOWEN. 1965. Fine structure of *Amphipleura pellucida*. II. Cytoplasmic fine structure and frustule formation. Amer. J. Bot. 52:1067–1078.

STOERMER, E. F., H. S. PANKRATZ, AND R. W. DRUM. 1964. The fine structure of *Mastogloia Grevillei* Wm. Smith. Protoplasma 59:1– 13.

STOSCH, H. A. VON. 1977. Observations on *Bellerochea* and *Streptotheca*, including descriptions of three new planktonic diatom species. Nova Hedwigia, Beih. 54:113–166.

———. 1981. Structural and histochemical observations on the organic layers of the diatom cell wall. Pp. 231–250 *in* Proceedings of the 6th Symposium on Recent and Fossil Diatoms, R. Ross, ed. O. Koeltz, Koenigstein.

TAYLOR, D. L. 1972. Ultrastructure of *Cocconeis diminuta* Pantocsek. Arch. Microbiol. 81:135–145.

WALKER, G. K., L. SICKO-GOAD, AND E. F. STOERMER. 1979. An ultrastructural examination of the pennate diatom *Caloneis amphisbaena*. Microbios Lett. 12:141–152.

WATSON, M. L. 1958. Staining tissue sections for electron microscopy with heavy metals. J. Biophys. Biochem. Cytol. 4:475– 478.

Explanation of Plates

Plate 1, Figures 1–7

FIGURES 1–7. *Encyonema caespitosum*. FIGURES 1–6 LM. FIGURE 1. Valve view showing shape, striae, and raphe features. Scale bar = 10 µm. FIGURES 2–6. growth habit. FIGURE 2. Cells crowded at tip of mucilaginous tube. FIGURE 3. Cells crowded at tip of tube, more distantly spaced away from tip. FIGURE 4. Cells within tubes distantly spaced and shown to be connected by mucilage strands. FIGURES 5, 6. Bumps or protrusions on tube. Scale bar in Figure 2 = 20 µm for Figures 2, 5, 6. Scale bar in Figure 3 = 10 m for Figures 3, 4. FIGURE 7. TEM, longitudinal section showing dorsal nucleus, ventral pyrenoid, vacuoles on either side of the nucleus and Golgi surrounding nucleus. Scale bar = 3 µm. Abbreviations used throughout: C = chloroplast; D = diatotepic layer; G = Golgi; I = interstriae; L = lipid; M = mitochondria; N = nucleus; Nu = nucleolus; P = pyrenoid; Pl = plasmalemma; R = raphe; S = subfrustular zone; T = mucilaginous tube; Va = vacuole; V1 = small, Golgi-derived vesicles; V2 = small fibrous vesicles; V3 = large, fibrous vesicles; V4 = dense fibrous vesicles; V5 = vesicles of the subfrustular zone.

Plate 2, Figures 8–12

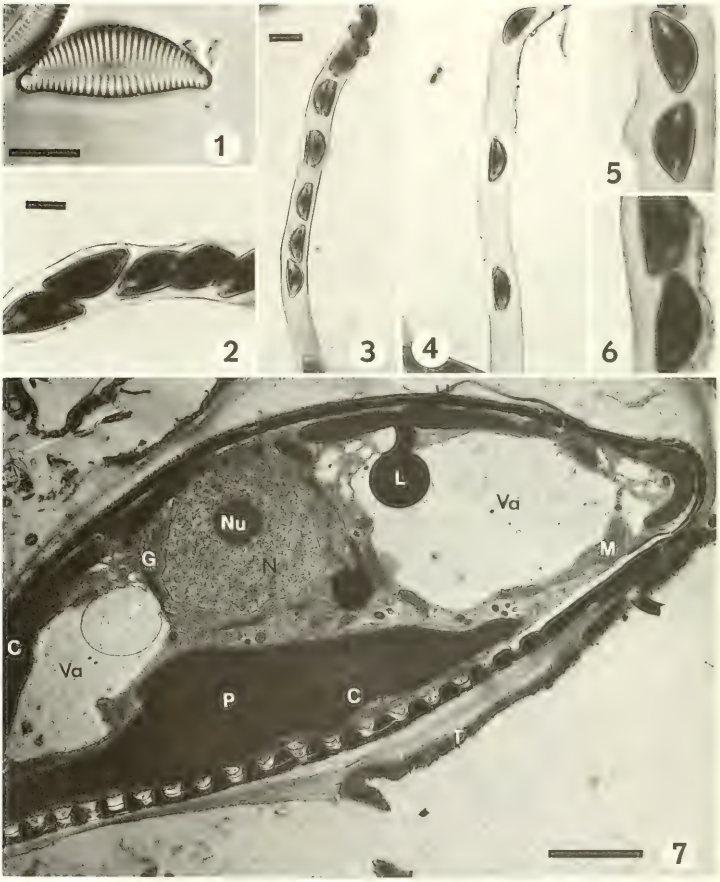
FIGURES 8–12. *Encyonema minutum*. FIGURES 8–10. LM. FIGURE 8. Valve view showing general morphological features. FIGURES 9, 10. Growth habit. Scale bars = 10 µm. FIGURES 11, 12. TEM. Transverse sections showing orientation of chloroplast, Golgi, nucleus, and vesicles. Scale bar in Figure 11 = 1 µm, scale bar in Figure 12 = 0.5 µm.

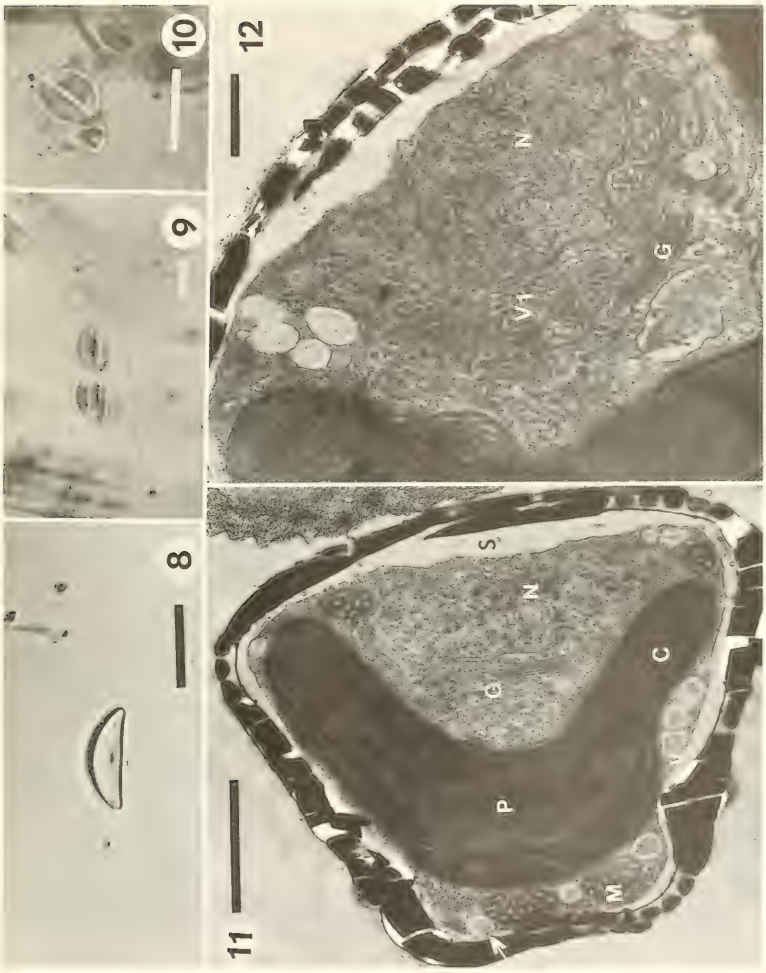
Plate 3, Figures 13–17

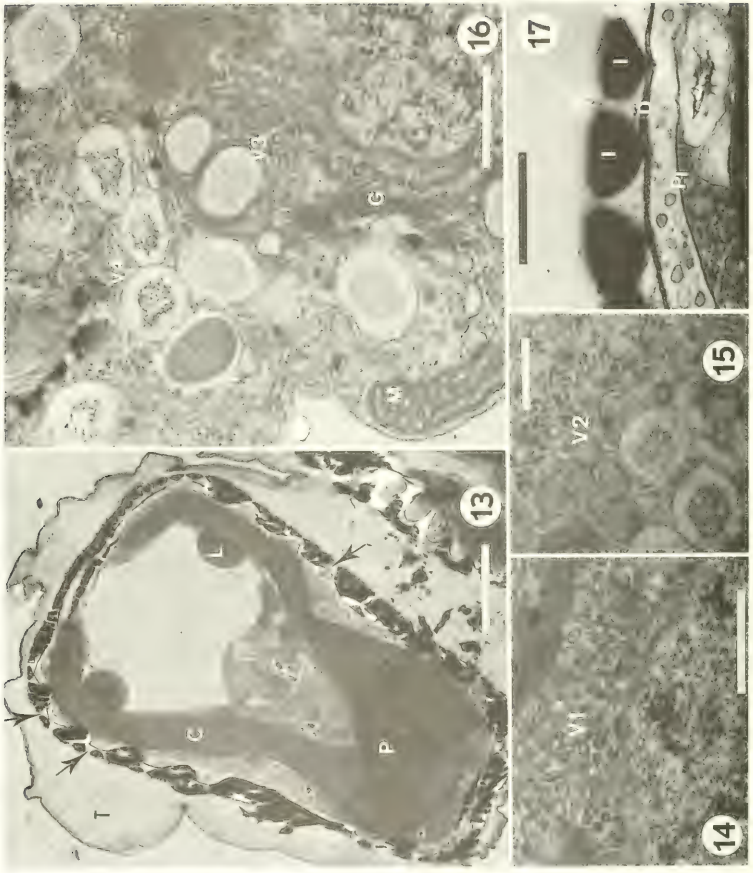
FIGURES 13–17. *E. caespitosum*, TEM. FIGURE 13. Longitudinal section showing orientation and position of chloroplast, pyrenoid, vacuole and vesicles. Diatotepic layer projects into puncta (arrows). Scale bar = 1 µm. FIGURE 14. V1 vesicles are small, of uniform density and found primarily around the central cytoplasm. Scale bar = 0.5 µm. FIGURE 15. V2 vesicles are fibrillar-like, with fibrils being of uniform density throughout. Scale bar = 0.25 µm. FIGURE 16. V3 and V4 vesicles have a central fibrillar mass and radiating strands. Central fibrillar material is more dense in the V4 vesicles. Scale bar = 0.5 µm. FIGURE 17. V5 vesicles located in the subfrustular zone between plasmalemma and diatotepic layer. Note V4 vesicle fusing with plasmalemma. Scale bar = 0.5 µm.

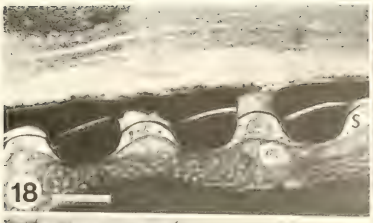
Plate 4, Figures 18–24

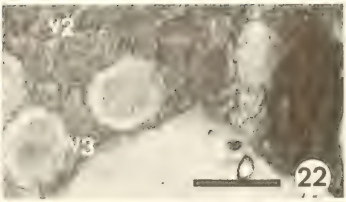
FIGURES 18–21. *E. caespitosum*, TEM. FIGURE 18. Diatotepic layer protrudes into puncta of valve face. Subfrustular zone, with V5 vesicles, is evident. Scale bar = 0.5 µm. FIGURES 19, 20. Sections with raphe, showing diatotepic layer fused with axial rib. In Figure 19 mucilage appears to be associated with the raphe (arrow). Scale bars = 0.5 µm. FIGURE 21. Transverse section showing tube of dense mucilaginous material and distinct layers. Scale bar = 1 µm. FIGURES 22–24. *E. minutum*, TEM. FIGURE 22. V2 and V3 vesicles showing differences in size and contents. Scale bar = 0.25 µm. FIGURE 23. V2 vesicles are shown fused with plasmalemma. Subfrustular zone has many V5 vesicles. Scale bar = 0.25 µm. FIGURE 24. Transverse section showing diatotepic layer fused to axial rib of raphe and valve mantle. Thickenings of diatotepum occur at interstriae. Mucilage covering of cell is also visible. Scale bar = 0.5 µm.


1
2
3
4
5
6
7
L
Va
Nu
G
N
M
C
Va
P
C

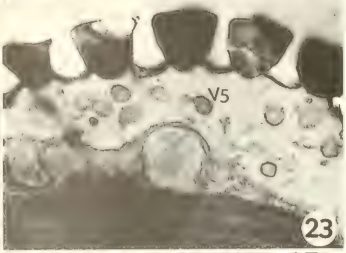

8
9
10
11
12
P
G
S
N
C
M
V1
N
G

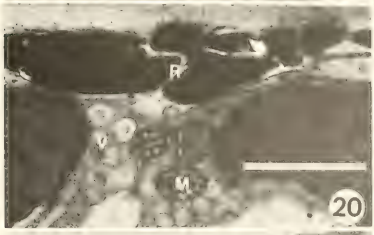

13
T
C
L
P
16
V1
V2
G
M
17
I
I
D
Pl
15
V2
14
V1

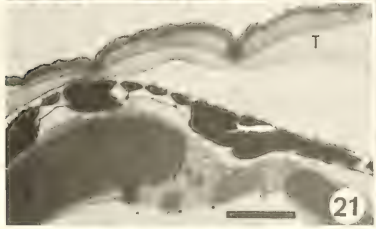

S
18

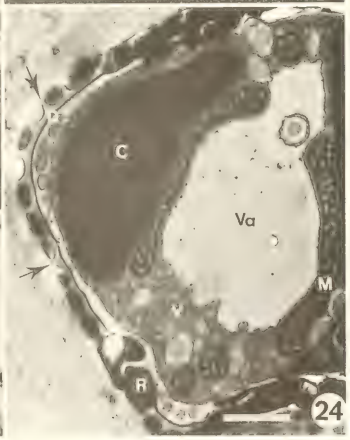

V2
V3
22

R
S
19


V5
23


R
V
M
20


T
21


C
Va
M
V
R
24

Ontogeny and Phylogeny in the Genus *Tetracyclus*

by

D. M. Williams

Botany Department, The Natural History Museum,
Cromwell Road, London, SW7 5BD, England

with 4 figures and 1 table

Abstract: Species in the genus *Tetracyclus* are largely classified according to the shape and size of their valves. The shape and size of diatom valves are dependent on a number of factors, where one of the most important is age relative to the time of auxosporulation. Auxospore valves of *Tetracyclus* are shown to exhibit two forms, either having a prominent central constriction or inflation. Evaluation of valve shape as a taxonomic character involves consideration of the changes that occur during the species life cycle and the constraints enforced during valve construction. Significance of shape can be sought in the clarification of factors affecting shape change (ontogeny) and the interrelationships of the species within the genus (phylogeny). Crucial to the understanding of shape change in the analysis of characters is the method of character representation. Taxonomic characters can be understood as either binary, multistate, or continuous. The effects of ontogeny on character phylogeny is discussed.

Introduction

The freshwater diatom genus *Tetracyclus* Ralfs has been the subject of taxonomic revision as it consists of a few extant and many extinct but well-preserved taxa with differing geographical and stratigraphical ranges (Williams 1987, 1989, 1990a; Williams and Li 1990). At present the genus contains at least 30 taxa: five are reported living (*T. glans* (Ehrenberg) Mills, *T. emarginatus* (Ehrenberg) W. Smith, *T. rupestris* (Braun) Grunow, *T. javanicus* Hust., and *T. ellipticus* var. *lancea* f. *chilensis* Krasske: Hustedt 1914a; Krasske 1939; Bourrelly and Manguin 1952; Williams 1987, and about 25 are reported as fossils only (Table 1; but see VanLandingham 1978:3981–3989 for a compilation of synonyms, many of which need investigation). In addition, there are a number of new or poorly described fossil species that require further investigation, probably increasing the total number of species in the genus to in excess of 40 (Williams and Li 1990).

Taxonomy of the genus *Tetracyclus* has to a greater extent relied almost exclusively on valve size shape and the frequency of valve characters such as striae and rib density (Hustedt 1914a; Li 1982, 1984). However, information is now emerging from auxospore and initial valves for both fossil and Recent taxa that allow life cycles changes to be either observed, in the case of extant taxa (Williams 1987), or inferred, in the case of fossil taxa (Williams 1990a).

	Auxospore	Post-auxospore	Valves	Pre-auxospore
	(1)		(1)	(2)
T. celatom	constriction		constriction	elliptical
	(1)		(1)	(2)
T. javanicus	constriction		constriction	elliptical
	(1)		(2)	(3)
T. "lancea"	constriction		elliptical	circular
	(1)		(2)	(2)
T. "chilensis"	constriction		elliptical	elliptical
	(4)		(4)	(2)
T. glans	inflation		inflation	elliptical
	(4)		(4)	(2)
T. pagesi	inflation		inflation	elliptical

FIGURE 1. Diagrammatic representation of valve shape change in a number of species from the genus *Tetracyclus*. The designations post- and pre-auxospore indicate the direction of size diminution (see also the arrow for reference). The figures in brackets above each shape designation is the arbitrary coding number used in Figures 2 and 3.

Characters used for the description of species are recorded from the siliceous parts of the valve, girdle, and auxospore and compared on the basis of their structure and position. It is now apparent, however, that characters develop from precursor elements during the organisms' life cycle and during the silicification process of valve construction. Hence, consideration of the mode of development (its ontogeny) is vital and can lead to a greater understanding of the relationship between different character states (e.g., Mann 1984; Kociolek and Williams 1987; Pickett-Heaps et al., 1990).

This paper presents a preliminary examination of the problems associated with using valve shape as a taxonomic character, broaching the subject from the perspective of ontogenetic development and phylogenetic position.

Materials and Methods

The morphological data used in this paper have been taken from a detailed study of *Tetracyclus* species and appear in a series of papers, either published, in press, or in preparation (Williams 1987, 1989, 1990a; Williams and Li 1990). At present only a few species are known in enough detail to determine the sequence of valve succession from primary cells to the onset of auxosporulation. For purposes of discussion, cells that arise immediately after auxosporulation are referred to as post-auxospore and cells that occur at the smallest size ranges are referred to as pre-auxospore; vegetative valves occur between these two stages.

Results

Preliminary examination of auxospore valves from species in *Tetracyclus* reveals two distinct types, either with a central inflation or with a central constriction (Williams 1987, 1990a).

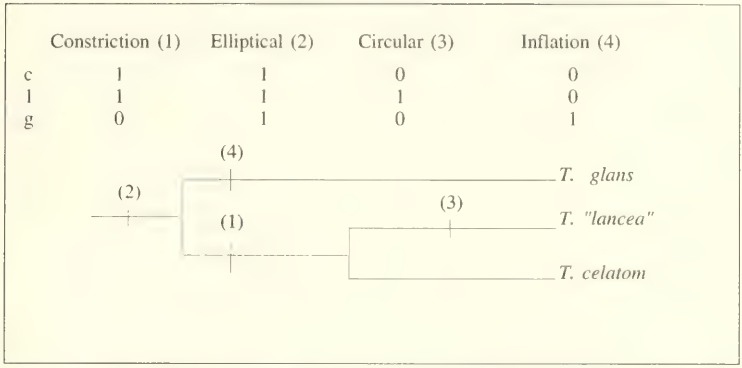


FIGURE 2. Upper diagram presents matrix of characters against taxa as binary variables; lower diagram is the character state tree constructed from these data. c = *T. celatom*, l = *T. lancea* and g = *T. glans*. The figure in brackets above each shape designation is the coding number. See text for further explanation.

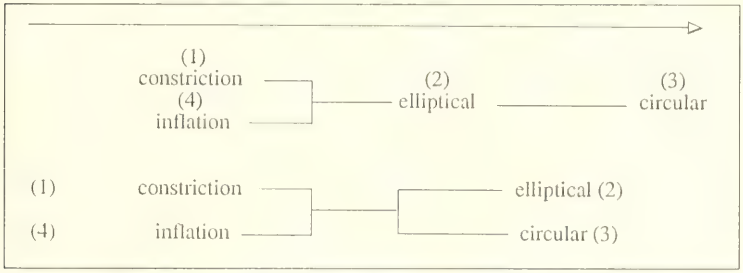


FIGURE 3. Upper diagram is a representation of valve shape change as a single multistate character with direction of change indicated by the arrow; lower diagram is the character state tree constructed from these data. The figure in brackets above each shape designation is the arbitrary coding number used in Figures 2 and 3.

Auxospore valves of *T. celatom* Okuno were discovered in a fossil deposit from Trout Creek, Oregon, U. S. A. They appear almost identical to fossil auxospores from *T. ellipticus* var. *lancea* (Ehrenb.) Hustedt in the German Hainsbach deposit, and both would be identified as *T. ellipticus* var. *constricta* Hustedt using conventional criteria (Williams 1990a). From observations based on other specimens in the same deposits, it was established that the valve outline of *T. celatom* alters only with respect to the relative distances between the central constriction and the polar inflations (Okuno 1958; Williams 1990a). Pre-auxospore valves assume an elliptical outline. Similarly, *T. javanicus*, often misidentified as *T. celatom*, develops in the same fashion (unpublished observations on type material; see also *T. ellipticus* var. *constricta* and *T. ellipticus* var. *apiculata* Okuno illustrated from Miocene fossil material in Okuno 1959:26). Conversely, *T. ellipticus* var. *lancea* and *T. ellipticus* var. *elongata* f. *chilensis* both have vegetative valves that assume an elliptical

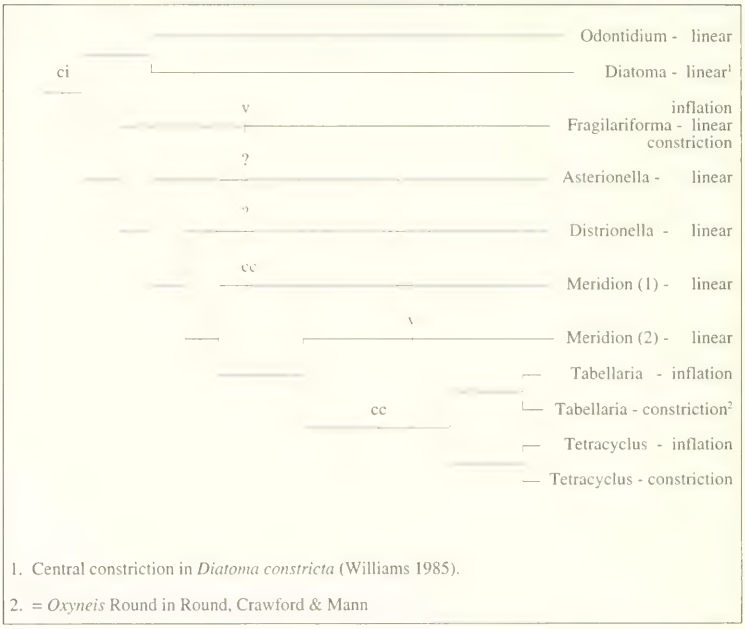


FIGURE 4. Cladogram based on the data in Williams (1990b). No change to the tree topology is observed when shape characters are added, either as binary variables (Fig. 2) or multistate variables (Fig. 3). Each genus splits into two parts, each characterised by the auxospore type. Abbreviations are: ci = central inflation; cc = central constriction; v = variable shape auxospore; ? = no knowledge or insufficient evidence.

outline early in development, retaining the shape throughout their life cycle, becoming circular in pre-auxospore valves only in the former (Williams 1990a and unpublished observations).

In contrast to the above species, *T. glans* has auxospore valves with a central inflation and vegetative valves retain the inflation, while the smallest valves become almost elliptical (Williams 1987). This situation is similar in the closely related, extinct species *T. pagesi* Héribaud, where the taxon described by Brun and Héribaud as *T. tripartitus* (in Héribaud 1893:223; see also Andrews, 1970:A10, Figs. 10, 11) is probably its auxospore. These observations are summarized in Figure 1.

It appears, then, that the "same" character (e.g., elliptical shape) occurs in different taxa at different times in their respective life cycles and begs the question: Is shape a single character? And if not, can shape be logically subdivided into meaningful states?

Characters can be described as one of three types (Platnick 1989; Farris 1990). The first type of character is called a binary character. Binary characters have a presence/absence relationship (for instance, in diatoms as a whole, the possession of a raphe) or an either/or

TABLE 1. Summary of species in the genus *Tetracyclus* and extent of knowledge. A number of these species still require further examination.

	Morphological data [1]			
	Valve	Girdle	Auxospore	Reference
Recent				
T. emarginatus	+	+	–	Williams 1987
T. rupestris	+	+	–	Williams 1987
T. lacustris	+	+	+	Williams 1987
?*T. "chilensis"* [2]	–	–	–	Not yet described
?*T. javanicus*	+	+	–	Hustedt 1914a
Fossil				
T. boryanus	+	–	–	Williams, in prep.
T. "castellum" [3]	+	–	–	Not yet described
T. celatom	+	+	+	Williams 1990a
T. clypeus	+	+	–	Williams 1989
T. cruciformis	+	–	–	Andrews 1970
T. divisium	+	–	–	Williams 1989
T. dunhuanensis	+	–	–	Li 1984
T. ellipticus	+	+	–	Williams, in prep.
T. excentricum	+	+	–	Williams 1989
T. "lata" [4]	+	+	+	Williams, in prep.
T. islandica	–	–	–	Not yet described
T. japonicus	+	+	–	Williams 1989
T. "lamina" [5]	+	–	–	Williams 1989
T. "lancea" [6]	+	+	–	Williams, in prep.
T. "linearis" [7]	+	+	–	Williams, in prep.
T. "ovalifolius" [8]	+	–	–	Li 1984
T. "ovaliformis"	+	–	–	Li 1984
T. pagesi	+	+	–	Williams, in prep.
T. "parvula" [9]	+	+	–	Williams, in prep.
T. peragallo	+	–	–	Not yet described
T. rostratus	+	–	–	Not yet described
T. subclypeus	+	–	–	Williams & Li 1990
T. subdivisium	+	–	–	Williams & Li 1990
T. stella	+	+	+	Williams, in prep.
T. stellare	–	–	+	Not yet described

1. Names in quotations are provisional.
2. = *T. ellipticus* var *lancea* f. *chilense* Krasske non *Biblarium chilense* Ehrenb.
3. = *T. castellum* (Ehrenberg) Grunow.
4. = *T. ellipticus* var. *lancea* f. *lata* Hustedt
5. = *T. ellipticus* var. *lamina* f. *lamina* (Ehrenberg) M. Peragallo
6. = *T. ellipticus* var. *lancea* (Ehrenberg) Hustedt
7. = *T. ellipticus* var. *linearis* (Ehrenberg) Hustedt.
8. = *T. ellipticus* var. *ovalifolius* Li
9. = *T. lacustris* var. *parvula* Forti

relationship (for instance, in raphid diatoms, the presence of a naviculoid or canal raphe). Binary characters are the most easily understood, as states are either present or they are not. The second type of character is a multistate character. Multistate characters have more than two states (such as the presence of different type of spines on the valve surface, cf. Williams 1985). The relationship between multistate and binary characters is not simply one of numbers as the former may require placing the states in some order. Finally, there are continuous characters (such as measurements or frequencies). The major difficulty with continuous characters is deciding the limits between and within states (Farris 1990). All three character types can be rendered binary with the appropriate coding procedure.

When considering the character of shape, Figure 2 presents a conventional data matrix for recording binary characters from which a character state tree has been constructed. Alternatively, Figure 3 presents the data as a multistate character. If the auxospore is considered the starting point, then there are two alternatives: valves with either a central inflation or constriction. Both alternatives pass through an "elliptical" stage, but only one species continues through to a circular stage. This can be represented as a character state tree with directional change (which is not equivalent to a phylogenetic tree) or a pair of bifurcating alternate routes (Figure 3). Finally, the sequence of change could be considered as a continuum because of the dynamic nature of ontogenetic change (Figure 1). To elucidate meaningful states may require investigations along the lines of morphometric analyses, a method that has not been explored further here but may be a fruitful line of investigation (Theriot, pers. comm.).

When considering the alternative character state trees, that based on the binary data matrix, while representing all the characters and their distributions, does not reflect the temporal sequence based on the multistate character constructed from ontogeny (compare Fig. 2 with Fig. 3). The conflict appears in the distinction between auxospores with inflated as opposed to constricted valves and the shape of pre-auxospore valve. This suggests that one auxospore type is derived relative to the other.

Discussion

Phylogeny

The roots of apparent contradiction can be sought first in the relationships of the genus *Tetracyclus* to other araphid diatoms and their auxospore types.

Tetracyclus is easily recognized by the presence of prominent, thick transapical ribs (costae *sensu* Patrick and Reimer 1966) and a well developed septum on a number of its girdle bands (Patrick and Reimer 1966; Williams 1987). However, transapical ribs occur in the closely related genera *Diatoma* Bory and *Meridion* C. A. Ag. (Williams 1985, 1990b), and septa occur in many other freshwater araphid diatoms (Round 1980). *Tetracyclus* is more accurately characterized by two morphological characters unique to it (Williams 1990b): (1) striae pattern becomes irregular and scattered towards the sternum; and (2) valvocopula and primary copulae have a multiple series of small poroids at the junction of the pars interior and pars exterior (Williams 1987, 1990b).

The genus *Tabellaria* Ehrenb. has for some time been considered the most closely related taxon to *Tetracyclus* (Patrick and Reimer 1966; Round et al. 1990). This has been supported by a cladistic character analysis of a number of freshwater and marine araphid diatoms (Williams, 1990b, Fig. 4). *Tabellaria* shares three unique characters with *Tetracyclus*: (1) the interconnection of the valve mantle forms an external lip; (2) the three-part girdle structure; and (3) a single pleural band (Williams 1987, 1990b).

Tabellaria consists of at least three freshwater species, although species level taxonomy is still controversial and opinions over recognizable taxa differ (Flower and Battarbee 1985; Lange-Bertalot 1988). Although the genus is not difficult to identify, many of the characters previously used to distinguish it from other freshwater araphid diatoms are proving to be unreliable in the determination of their interrelationships (Williams and Round 1987, 1988; Williams 1990b). Round (in Round et al. 1990) has recently placed *Tabellaria binalis* (Ehrenb.) Grun. in the new genus *Oxyneis* Round. *Tabellaria binalis* differs from other species of *Tabellaria* by possessing considerably smaller valves, which are either linear (as in *T. binalis* var. *capitata* Flower) or with a central constriction, rather than the typical *Tabellaria* central inflation (Flower and Battarbee 1985; Lange-Bertalot 1988).

Of the three unique characters that support the sister group relationship between *Tabellaria* and *Tetracyclus*, *Tabellaria binalis* possesses the external valve lip and has girdle bands typical for *Tabellaria* and *Tetracyclus* (compare Flower 1989:22, Fig. 1 with illustrations in Williams 1987, 1989). It has not been possible to detect the single pleural band (pers. obs.) but the above two characters do not support the erection of the genus *Oxyneis*. This has important consequences. If *Tabellaria* is characterized so as to exclude *T. binalis* then it is composed only of species with valves exhibiting a central inflation and, although the auxospores are unknown (but see Mann 1988), would suggest that species of *Tetracyclus* with the central inflation are primitive. This would contradict the evidence as presented by the binary coding (Fig. 2). However, with the inclusion of *Tabellaria binalis*, either the central constriction or the inflation could be relatively primitive to the other. It is worth noting that the unusual fossil species *T. celatom* Khursevich is clearly related to *T. binalis* and was described along with a variety *elongata* that is clearly an auxospore valve and lends support to this thesis (Khursevich 1982). Thus, although sister taxon relationships are fairly well established, they offer no unequivocal conclusion.

ONTOGENY

Alternatively, constraints imposed by formation of the auxospore that affect the shape of its valve can be sought in ontogeny (Mann 1984). For instance, in a study on the auxospore of *Rhoicosphenia*, Mann (1982) noted that the perizonium has a marked effect on the form of the initial cell and hence on all succeeding generations derived from that valve. In *Rhoicosphenia* there is a closed primary transverse girdle that probably dictates the size of the largest possible specimens. In addition, the number of transverse bands will constrain areas of valve silicification. Thus, in *Tetracyclus*, auxospore valves of the type with a central inflation may be the result of perizonal transverse bands forming at each pole constraining the "growth" at these areas, while those with the central constriction may be the result of central perizonal transverse bands only, constraining "growth" at the center and allowing the valve to expand at the poles, or at least towards the polar regions.

In other araphid diatoms the situation is similar. In *Diatoma* and *Odontidium*, for instance, auxospores observed so far all exhibit valves with a central inflation (Williams 1985, with the exception of *D. constricta* (Grun.) Williams). However, the initial cells from *Fragilariforma virescens* (Ralfs) Williams & Round occur in a myriad of shapes before finally assuming the vegetative valve morphology (Hustedt 1914b) as does the heteropolar species of the closely related genus *Meridion* (Geitler 1932). Observations on the auxospores and initial cell structure of *F. virescens* show no sign of transverse bands, although longitudinal bands are evident (unpublished observations), hence the shape of the auxospore valves remain unconstrained.

RESOLUTION

Resolving the position of shape change is one of accurate character coding and logical analysis, combining both the information gained from ontogeny and phylogeny.

It is popular to order both multistate and binary character states according to perceptions of either phylogenetic, ontogenetic, or stratigraphic change (Kociolek 1986, Wiley 1981). Determination of the polarity of character states using the temporal ontogenetic sequence implies acceptance of Haeckel's doctrine of "ontogeny recapitulating phylogeny," a theory now given little credence among comparative biologists as a generalization (Gould 1977). Determination of the polarity of character states using stratigraphic occurrence presents the unsolvable problem of the reliability of the fossil record (Schoch 1986). However, allowing characters to remain unordered requires that the analysis determines the order against the outcome of other character distributions (Platnick 1989).

As the sister taxon relationships between *Tetracyclus* and *Tabellaria* are fairly well established, when the characters for shape change are added to the morphological data matrix of Williams (1990b), either in binary or multistate form, they support the proposition that auxospore valves with a constriction are primitive relative to those with the inflation (Fig. 4). This conclusion does not contradict either the character state tree based on the distribution of shapes among species (Fig. 2) or the ontogenetic order with which they emerge (Fig. 3).

The possibility that valves from different parts of the life cycle can have alternative outlines has not been considered in detail for *Tetracyclus*. Observing a new shape to the valve outline has largely prompted the erection of new taxa. However, appreciation of the potential intergrading of the various shapes has prompted complex representations of species interrelationships (Hustedt 1914a). Conversely, because the species are so obviously "similar" in outline, it has also prompted the suggestion that they are simply forms of one another and could be a single species (Round et al. 1990).

Valve shape is often considered to be a single character but is clearly the result of a number of different interactions during valve morphogenesis (Schmid 1979). Notwithstanding this kind of approach, it appears constructive to consider shape as a character resulting from these interactions. Such characters are usually expressed as a series of alternatives: elliptical, circular, lanceolate, cruciform, polygonal, or variations thereof. The implication is that these are alternatives of a single character. Ontogeny reveals that characters may not be alternatives of each other but successive stages of each other (Williams 1990a). In either case, it appears not to matter whether these are treated as separate states or separate characters; what does matter is if the attributes correspond with characters that suggest the same groups (Patterson 1982).

Literature Cited

ANDREWS, G. W. 1970. Late Miocene nonmarine diatoms from the Kilgore Area, Cherry County, Nebraska. U. S. G. S. Prof. Pap. 683-A:A1–A22.

BOURRELLY, P. AND E. MANGUIN. 1952. Algues d'eau douche de la Guadeloupe de dependences. Centre National de la Recherche Scientifique, Societe d'Edition d'-Enseignement Superieur, Paris.

FARRIS, J. S. 1990. Phenetics in camouflage. Cladistics, 6:91–100.

FLOWER, R. J. 1989. A new variety of *Tabellaria binalis* from several acid lakes in the U. K. Diatom Res. 4:21–23.

FLOWER, R. J. AND R. W. BATTARBEE. 1985. The morphology and biostratigraphy of *Tabellaria quadriseptata* (Bacillariophyceae) in acid waters and lake sediments in Galloway, Southwest Scotland. Br. Phycol. J. 20:69–79.

GEITLER, L. 1932. Der Formweschel der pennaten Diatomeen (Kieselalgen). Arch. Protistenk. 78:1–226.

GOULD, S. J. 1977. Ontogeny and Phylogeny. Belknap Press, Harvard University Press.

HÉRIBAUD, J. 1893. Les Diatomées Auvergne. Libraries des Science Naturelles, Paris. 233 pp.

HUSTEDT, F. 1914a. Die Bacillariaceen-Gattung *Tetracyclus* Ralfs; kritische Studien über Bau und Systematik der bisher beschriebenen Formen. Abh. Naturw. Ver. Bremen 23:90–107.

———. 1914b. Bacillariales aus den Sudeten und einigen benachbarten Gebieten des Odertales. Arch. Hydrobiol. Planktonk. 10:1–128.

KHURSEVICH, G. K. 1982. Neogene diatom assemblages from Byelorussia and their stratigraphic significance. Acta Geol. Acad. Sci. Hungaricae 25:123–134.

KOCIOLEK, J. P. 1986. Determining character polarity in diatoms: An alternative approach. Diatom Res. 1:189–192.

KOCIOLEK, J. P. AND D. M. WILLIAMS. 1987. Unicell ontogeny and phylogeny: examples from the diatoms. Cladistics 3:274–284.

KRASSKE, G. 1939. Zur Kieselalgenflora Südchiles. Arch. Hydrobiol. 31:349–468.

LANGE-BERTALOT, H. 1988. Die Gattung *Tabellaria* unter besonderer Berücksichtigung an *Tabellaria ventricosa* Kützing (Bacillariophyceae). Nova Hedwigia 46:413–431.

LI, J-Y. 1982. Genus *Tetracyclus* and its stratigraphic significance. Bull. Inst. Geol. Chinese Acad. Geol. Sci. 5:149–167.

———. 1984. Some new species and varieties of the genus *Tetracyclus* Ralfs (Bacillariophyta). Acta Phytotax. Sinica 22:231– 236.

MANN, D. G. 1982. Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). II. Auxospore formation and perizonium structure of *Rh. curvata*. J. Phycol. 18:264–274.

———. 1984. An ontogenetic approach to diatom systematics. Pp. 113–144 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

———. 1988. Why didn't Lund see sex in *Asterionella*? A discussion of the diatom life cycle in nature. Pp. 385–412 *in* Algae and the aquatic environment, F. E. Round, ed. Biopress Ltd, Bristol.

OKUNO, H. 1958. Electron-microscope fine structure of fossil diatoms. IV. Observations on some diatoms found in the "Celatoms." Trans. Proc. Paleont. Soc. Japan 31:237–242.

———. 1959. Diatomaceous Earth in Sentana-cho-, Hokkaido III. J. Jap. Bot. 34:25–29.

PATTERSON, C. 1982. Morphological characters and homology. Pp. 21–74 *in* Problems of phylogenetic reconstruction, K. A. Josey and A. E. Friday, eds. Academic Press, London and New York.

PATRICK, R. AND C. W. REIMER. 1966. The diatoms of the United States, Vol. 1. Acad. Nat. Sci. Phila. Monogr. No. 13. 688 pp.

PICKETT-HEAPS, J. D., A.-M. M. SCHMID, AND L. A. EDGAR. 1990. The cell biology of diatom valve formation. Prog. Phycol. Res. 7:1–168.

PLATNICK, N. 1989. Cladistics and phylogenetic analysis today. Pp. 17–24 *in* The Hierarchy of Life, B. Fernholm, K. Bremer and H. Jörnvall, eds. Elsvier Science Publishers, B. V.

ROUND, F. E. 1980. The diatom genus *Climacosphenia* Ehrenberg Bot. Mar. 25:519–527.

ROUND, F. E., R. C. CRAWFORD, AND D. G. MANN. 1990. The diatoms. Cambridge University Press.

SCHMID, A.-M. M. 1979. The development of structure in the shells of diatoms. Nova Hedwigia, Beih. 64:219–236.

SCHOCH, R. M. 1986. Phylogeny reconstruction in palaeontology. Van Nostrand Reinhold, New York.

VANLANDINGHAM, S. L. 1978. Catalogue of the fossil and Recent genera and species of Diatoms and their synonyms. Part 7. J. Cramer, Vaduz.

WILEY, E. O. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. J. Wiley and Sons, N. Y.

WILLIAMS, D. M. 1985. Morphology, taxonomy and inter-relationships of the ribbed araphid diatoms from the genera *Diatoma* and *Meridion* (DiatomaceaeBacillariophyta). Bibl. Diatomologica 8:1–228.

———. 1987. Observations on the genus *Tetracyclus* Ralfs (Bacillariophyta) I. Valve and girdle structure of the extant species. Br. phycol. J. 22:383–399.

———. 1989. Observations on the genus *Tetracyclus* Ralfs (Bacillariophyta) II. Morphology and taxonomy of some species from the genus *Stylobiblium*. Br. phycol. J. 24:317–327.

———. 1990a. Examination of auxospore valves in *Tetracyclus* from fossil specimens and the establishment of their identity. Diatom Res. 5:189–194.

———. 1990b. Cladistic analysis of some freshwater araphid diatoms with particular reference to *Diatoma* and *Meridion*. Pl. Syst. Evol. 171:89–98.

WILLIAMS, D. M. AND J-Y. LI. 1990. Observations on the genus *Tetracyclus* Ralfs (Bacillariophyta) III. Description of two new species from Chinese fossil deposits. Br. phycol. J.

WILLIAMS, D. M. AND F. E. ROUND. 1987. Revision of the genus *Fragilaria*. Diatom Res. 2:267–288.

———. 1988. Phylogenetic systematics of *Synedra*. Pp 303–315 *in* Proceedings of the 9th International Diatom Symposium, F. E. Round, ed. Biopress Ltd., Bristol and Koeltz Scientific Books, Koenigstein.

Evolution and Phylogeny of Some Diatom Genera of the Class Centrophyceae

by

Galina K. Khursevich

Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Zhodinskaya street 7, 220600 Minsk, Byelorussia

with 4 plates

Abstract: Electron-microscopic investigations of valves of the genera *Actinocyclus*, *Undatodiscus*, and *Lobodiscus* reveal that these genera share close phylogenetic relationships. Within this lineage, evolution has occurred in the following ways: increase in assimilating surface of the frustule, change from loculate areolae with one-sided external cribrum to loculate areolae with two-sided velum, increased complexity of rimoportulae morphology, and development of unique structures. Interrelationships and evolution of this group are presented and discussed.

Introduction

Several diatom species of biostratigraphic significance were originally described as members of the genus *Coscinodiscus* from freshwater fossil deposits of Oligocene and Miocene ages in different regions of the former U. S. S. R. and western Europe (Krasske 1934; Sheshukova-Poretskaya and Moisseeva 1964; Rubina 1967, 1976). These taxa were referred to the newly erected genus *Pontodiscus* Temnisk. & Shesh. by Temniskova-Topalova et al. (1981). Bradbury (1984), using data obtained from scanning electron microscopy (SEM), suggested the transfer of *Pontodiscus miocenicus* (Krasske) Shesh. & Moiss. and *Coscinodiscus* sp. cf. *gorbunovii* Shesh., species found in the Middle Miocene sediments of the Poison Creek Formation, Snake River Basin, U. S. A. (Bradbury and Krebs 1982), to *Actinocyclus*. Additional *Actinocyclus* species have been found from Miocene deposits in China and the United States (Bradbury et al. 1984; Bradbury 1984).

Examination with SEM of all freshwater representatives of *Pontodiscus* (= *Coscinodiscus*) found in the former U. S. S. R. has confirmed that they belong to *Actinocyclus*. An exception is the extinct taxa *Coscinodiscus lobatus* var. *sibericus* Tscher (Tscheremissinova 1971:54–56, Pl. I, Figs. 7–9), ultrastructural features of which have permitted proposal of the new freshwater genus *Lobodiscus Lupik. & Churs.* (Lupikina & Khursevich, in press). Another genus with possible close affinities to *Actinocyclus* and *Lobodiscus* is *Undatodiscus* Lupik., a genus based on *Aulacodiscus variabilis* Lupik.

The present report reviews the ultrastructure of members of *Actinocyclus*, *Lobodiscus*, and *Undatodiscus* and examines their stratigraphic and phylogenetic relationships.

Materials and Methods

The freshwater *Actinocyclus* species were studied in numerous samples from the Oligocene and Miocene sediments of different regions of Siberia and the Far East. *Undatodiscus* taxa originated from Lower Miocene deposits of West Siberia and Upper Miocene deposits of Kamchatka. *Lobodiscus* species originated from the Middle-Upper Miocene diatomaceous rocks of the Tunkin hollow, located southwest of Lake Baikal. In most cases, type material was examined.

Besides diatoms, sediments studied from West Siberia have been dated by pollen and spores, as well as leaf and seed floras. The Neogene rocks of Kamchatka and the Primorie have been dated by palaeomagnetic investigations. The age of the Tunkin hollow's Tankhoi (formerly coal-bearing) suite and of the Vitim plateau's Dzhilinda suite has been confirmed by K-Ar dating of basalts underlying or overlying the rocks of these suites. The definitions of absolute age indicate that the lower boundary of the Tanchoi suite does not exceed the limits of the first half of Early Miocene (17.9–19.3 million years ago), and the end of the Dzhilinda suite formation took place not later than the Late Miocene (at about 13.2 my) (Stratigraphy of the USSR, 1986).

Preparation of samples for light microscopy (LM) has been carried out using standard methods adopted in the former U. S. S. R. For SEM, specimens were sputter-coated with gold and observed with a JEOL-35C. Terminology follows that recommended by Ross et al. (1979) and in Diatom Algae of the USSR (Fossil and Recent) (1988).

Results

Valve ultrastructure of representatives of the freshwater genera *Actinocyclus*, *Undatodiscus*, and *Lobodiscus* reveals close phylogenetic relationships between them. Their ecological, geographical, and stratigraphical distributions also suggest a close affinity between these genera. *Actinocyclus*, *Undatodiscus*, and *Lobodiscus* share morphological features of a short, cylindrical frustule, arrangement of loculate areolae in radial rows forming distinct or indistinct fascicles on the valve face surface, a marked difference between the areolate structure of the valve face and the mantle, marginal ring of large rimoportulae, and a single pseudonodulus in the submarginal zone of the valve.

Actinocyclus, the species of which inhabit marine and freshwater basins from the Oligocene, is ancestral to *Undatodiscus*. *Actinocyclus* valves (Figs. 1–13) are penetrated by loculate areolae with external cribra and internal foramina. A marginal ring of rimoportulae is located in the base of long or short hyaline rays on the boundry of the face and mantle, or on the valve mantle proper. Externally rimoportulae are represented by not only openings, which lie almost flush with the valve surface, but also tubular extensions.

Actinocyclus tubulosus Churs. is characterized by long, external tubes of rimoportulae located on the same level as the conic spines (Khursevich et al. 1990), while *A. delicatus* Lupik. & Churs. has short, external tubes and lacks spines (Khursevich and Lupikina, in press). Some freshwater *Actinocyclus* taxa have a rather wide hyaline ring with irregularly placed, conical (*A. trapeziformis* (Rub.) Rub. & Churs. var. *trapeziformis* etc.) or lobed (*A. lobatus* (Rub.) Rub. & Churs.) spines on the valve face-mantle junction (Rubina and Khursevich, 1990; Khursevich and Rubina, in press). *Actinocyclus ligularis* Churs. & Lupik. is distinguished by the development of ligula-shaped projections on the distal rim of the valve mantle.

Thus, invasion of *Actinocyclus* species into continental freshwater basins was accompanied by intensive speciation and the formation of the various individual adaptations to environmental conditions mentioned above.

The freshwater genus *Undatodiscus* (Figs. 14–19) evolved from the genus *Actinocyclus* in the Early Miocene. Its characteristic feature is the development of distinctly expressed dome-like convexities (concavities on the internal valve surface) in the radial undulation zone in the periphery of the valve face. Loculate areolae with external unbroken cribra and internal foramina sometimes have poorly developed volae with attached membranes without visible pores. These are poorly preserved in fossil taxa (Bratzeva et al. 1984: p. 275, Pl. 82, Figs. 5–9). Rimoportulae are placed in convexities. Their internal expression is of a comparatively long, narrow tube with an expanded, fan-shaped end, just as in *Actinocyclus*. The external expression of the rimoportula in the Early Miocene species *U. tubiformis* Rub., Lupik. & Churs. is also represented by a relatively high tube, penetrating the thin-wall, trapezium-like process with the cribrum structure (Lupikina et al., in press). The rimoportula of the Late Miocene species *U. variabilis* (Lupik.) Lupik. has a small round opening near the apical part of the dome-like convexity. More or less long hyaline rays or hyaline fields, formed by several merged hyaline rays, extend from rimoportulae toward the center of the valve in *U. variabilis*. Presence of the pseudonodulus on the valve face-mantle junction, development of the marginal ring of large rimoportulae, and other morphological features relate *Undatodiscus* to the family Hemidiscaceae Hendey *emend* Simonsen (Simonsen 1975).

The freshwater genus *Lobodiscus* (Figs. 20–25) is the more evolutionary advanced of the three, having separated from the genus *Undatodiscus* (but the possibility of its separation from the genus *Actinocyclus* is not excluded) in the Middle Miocene. Valve ultrastructure in this genus includes loculate areolae of three types. These include: (1) loculate areolae with two-sided velum (the internal, domed one and the external, unbroken cribrum) located in a single layer on the valve face surface; (2) mainly half-closed loculate areolae with the external cribrum; and (3) half-closed loculate areolae with the internal, domed velum placed in two layers and developed on the valve mantle. The pseudonodulus occurs on the boundary of the valve face surface and the valve mantle. The marginal ring of rimoportulae is associated with lobed spines, which may add greater surface area and thus buoyancy or may help link valves together. Rimoportulae have a long narrow tube internally with a shoe-shaped slit expressed in the apical part. This forms a right angle with the tube axis. Slit of the rimoportula in *Actinocyclus* and *Undatodiscus* species occurs usually in the same plane with the tube. Externally, rimoportulae are represented by very short tubes, expressed on the valve mantle directly under the lobed spines, or by long tubes penetrating the lobed spines. The lobed spines often resemble unbroken cribrum of the areolae on the external valve face surface.

Thus, diagnostic features of the genus *Lobodiscus* include development of three types of loculate areolae, their two-layer location on the valve mantle, complex morphology of rimoportulae, and the presence of linking (to all probability) lobed spines. There is sufficient evidence for classifying it as the type genus of the new independent monotypic family Lobodiscaceae Lupik. & Churs. (Lupikina and Khursevich, in press).

Actinocyclus, *Undatodiscus*, and *Lobodiscus* appear closely related, forming one of the phylogenetic lines of centric diatoms. Evolution of this group of genera has been realized in three features: increased assimilating surface of the frustule by formation of numerous dome-like convexities in the submarginal zone of the valve; change in areolae from loculate areolae with one-sided external cribrum (e.g., *Actinocyclus*) to loculate areolae with two-sided velum: the internal domed velum and the external unbroken cribrum (e.g., *Lobodis-*

cus); and specialization of external morphology of rimoportulae represented by a long tube penetrating the thin-wall process with cribrum ultrastructure (e.g., one *Undatodiscus* species) or possibly serving a linking function (e.g., *Lobodiscus*).

Discussion

According to electron microscopic investigations, the closest relationship of the family Hemidiscaceae has been observed with the marine genus *Azpeitia* Perag., which is known from the Eocene (Fryxell et al. 1986; Sims et al. 1989). Simonsen (1975) expressed an alternative opinion, suggesting a genetic relationship of the family Hemidiscaceae with the genus *Coscinodiscus* Ehrenberg (with the group "C" species), which possesses a small ring of marginal rimoportulae. Features characteristic of *Azpeitia* include several hyaline girdle bands with a wide valvocopula; a distinctive areolae structure of the valve mantle differing from that on the valve face; presence of loculate areolae with internal foramina and external cribra; a single large, nearly central rimoportula; and marginal ring of large rimoportulae.

Observations presented in this report lead to the suggestion that *Actinocyclus* was separated from the genus *Azpeitia*, apparently, in the Oligocene in the ocean, and subsequently underwent an adaptive radiation. *Actinocyclus* evolved both in oceans and seas and in freshwater basins. Freshwater *Actinocyclus* species are mostly widespread in the Miocene, continental sediments of the northern hemisphere in the middle latitudes (especially on the territory of the former U. S. S. R. and the United States). They are extinct and can be used as stratigraphic markers. Maximum development of the freshwater *Actinocyclus* taxa was recorded in the Middle Miocene of the western United States (Krebs et al. 1987). Order of appearance in the geological record of the freshwater *Actinocyclus* species in different regions of the former U. S. S. R is as follows:

A. antiquus (Rub.) Rub. & Churs.—Oligocene

A. tener (Rub.) Rub. & Churs.—Oligocene

A. trapeziformis (Rub.) Rub. & Churs. with varieties—Late Oligocene

A. lobatus (Rub.) Rub. & Churs.—Early Miocene

A. gorbunovii (Sheshuk.) Moiss. & Sheshuk.—Miocene

A. krasskei Bradbury & Krebs—Miocene

A. delicatus Lupik. & Churs.—Late Miocene

A. ligularis Churs. & Lupik.—Late Miocene

A. tubulosus Churs.—Late Miocene

Following Bradbury (1984), I suggest the following diagnostic features for classifying species within *Actinocyclus*: (a) character and density of areolae located on the valve face surface (in indistinct or distinct fascicles formed by long radial rows of areolae or by a combination of areolae radial rows and long or short hyaline rays running from rimoportulae toward the center of the valve); (b) structure, placement, and number of rimoportulae (morphology of both an internal and an external expressions of rimoportulae); (c) development of special structures (ligula-shaped projections; differences in the form of spines; definite type of pseudonodulus).

Acknowledgements

I would like to thank E. G. Lupikina, A. I. Moisseeva, N. V. Rubina, and E. A. Tscheremissinova for providing material from their collections, as well as for the discussion on the morphology of the genera considered here. I am grateful to hab. Z. I. Gleser for the critical comments on the genus *Lobodiscus*. Thanks are also due to S. A. Fedenya for technical assistance in the work.

Literature Cited

BRADBURY, J. P. 1984. Fossil *Actinocyclus* species from freshwater Miocene deposits in China and the United States. Pp. 157– 171 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

BRADBURY, J. P., K. V. DIETERICH, AND J. L. WILLIAMS. 1985. Diatom flora of the Miocene lake beds near Clarkia in northern Idaho. Late Cenozoic History of the Pacific Northwest. Pac. Div. Am. Assoc. Adv. Sci. 33–59.

BRADBURY, J. P. AND W. N. KREBS. 1982. Neogene and Quaternary lacustrine diatoms of the western Snake River Basin, Idaho-Oregon, U. S. A. Acta Geol. Acad. Sci. Hungaricae 25:97–122.

BRATZEVA, G. M., G. I. VITUKHIN, AND R. E. GITTERMAN. 1984. Atlas fauna i flora neogenovykh otlozheny Dalnego Vostoka. Tochilinsky oporny razrez Zapadnoi Kamchatki. M., Nauka, 335 pp.

DIATOM ALGAE OF THE USSR (FOSSIL AND RECENT). 1988. Vol.II (1). Leningrad, Nauka, 116 pp.

FRYXELL, G. A., P. A. SIMS, AND T. P. WATKINS. 1986. *Azpeitia* (Bacillariophyta). Related genera and promorphology. Syst. Bot. Monogr. 13:1–74.

KHURSEVICH, G. K. AND E. G. LUPIKINA. In press. New freshwater species of *Actinocyclus* (Bacillariophyta) from the Upper Miocene sediments of Kamchatka. Botanichesky Zhurnal.

KHURSEVICH, G. K., A. I. MOISSEEVA, T. F. KOZYRENKO, AND N. V. RUBINA. 1990. New taxa of the genus *Actinocyclus* (Bacillariophyta) from the Neogene freshwater sediments of the U. S. S. R. Bot. Zh. 75:1439–1442.

KHURSEVICH, G. K. AND N. V. RUBINA. In press. New combination of the genus *Actinocyclus* Ehrenberg (Bacillariophyta) from the Lower Miocene sediments of West Siberia. Botanichesky Zhurnal.

KRASSKE, G. 1934. Die Diatomeenflora der Hessischen Kiesselgurlager. Sitzungsber. Heidelb. Akad. Wiss. Math.-naturwiss. Kl. 5:3–27.

KREBS, W. N., J. P. BRADBURY, AND E. THERIOT. 1987. Neogene and Quaternary lacustrine diatom biochronology, Western U. S. A. Palaios 2:505–513.

LUPIKINA, E. G. AND G. K. KHURSEVICH. In press. Lobodiscaceae-novoe semeistvo distomovykh vodoroslei klassa Centrophyceae. Paleontologichesky Zhurnal.

LUPIKINA, E. G., G. K. KHURSEVICH, AND N. V. RUBINA. In press. The supplemented diagnosis and taxonomic position of the genus *Undatodiscus* in the system of Bacillariophyta. Botanichesky Zhurnal.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An emended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

RUBINA, N. V. 1967. Novye vidy roda *Coscinodiscus* Ehrenberg iz Turtasskoi svity Zapadno–Sibirskoi nizmennosti. Nov. Syst. Plant. Non–Vasc. 4:63–68.

———. 1976. Novye i redkie vidy rodov *Coscinodiscus* Ehrenberg i *Aulacodiscus* Ehrenberg iz kontinentalnykh verkhneoligozenovykh i nizhnemiozenovykh otlozheny Zapadno-Sibirskoi nizmennosti. Nov. Syst. Plant. Non-Vasc. 13:54–59.

RUBINA, N. V. AND G. K. KHURSEVICH. 1990. New representatives of the genus *Actinocyclus* (Bacillariophyta) from the Late Oligocene of West Siberia. Bot. Zh. 75:1565–1567.

SHESHUKOVA-PORETSKAYA, V. S. AND A. I. MOISSEEVA. 1964. Novye i interesnye presnovodnye diatomovye vodorosli iz neogena Zapadnoi Sibiri i Dalnego Vostoka. Nov. Syst. Plant. Non-Vasc. 1:92–103.

SIMONSEN, R. 1975. On the pseudonodulus of the centric diatoms, or Hemidiscaceae reconsidered. Nova Hedwigia, Beih. 53:83–94.

SIMS, P. A., G. A. FRYXELL, AND J. G. BALDAUF. 1989. Critical examination of the diatom genus *Azpeitia*: species useful as stratigraphic markers for the Oligocene and Miocene epochs. Micropaleontology 35:293–307.

STRATIGRAPHY OF THE USSR. THE NEOGENE SYSTEM. 1986. Vol. 2. M., Nedra, ed. 443 pp.

TEMNISKOVA–TOPALOVA, D. N., T. F. KOZYRENKO, A. I. MOISSEEVA, AND V. S. SHESHUKOVA-PORETSKAYA. 1981. The new genus *Pontodiscus* (Bacillariophyta). Bot. Zh. 66:1308–1311.

TSCHEREMISSINOVA, E. A. 1971. Novye i interesnye vidy diatomovykh vodoroslei iz neogena Pribaikalia. Nov. Syst. Plant. Non-Vasc. 8:52–66.

Explanation of Plates

Plate 1, Figures 1–6

FIGURES 1, 2. SEM. *Actinocyclus gorbunovii*, specimens from the Upper Miocene sediments of the Tym river basin, West Siberia. FIGURE 1. External valve surface with areolae cribra, a single pseudonodulus, and the marginal ring of rimoportulae on the mantle. FIGURE 2. Internal valve surface with areolae foramina, a single pseudonodulus, and marginal ring of rimoportulae. FIGURES 3, 4. SEM. *Actinocyclus tubulosus*, specimens from the Upper Miocene sediments of the Tym river basin, West Siberia. FIGURE 3. External valve surface with areolae cribra, long tubular extensions of rimoportulae (arrow) located on the same level with the conic spines. FIGURE 4. Internal valve surface with areolae foramina, a single pseudonodulus, and the marginal ring of rimoportulae. FIGURES 5, 6. SEM. *Actinocyclus ligularis*, specimens from the Upper Miocene sediments of West Kamchatka. FIGURE 5. Detail of the external valve surface with the ligula- shaped projection on the distal rim of the mantle. FIGURE 6. Detail of the internal valve surface with the ligula-shaped projection and the marginal ring of rimoportulae.

Plate 2, Figures 7–13

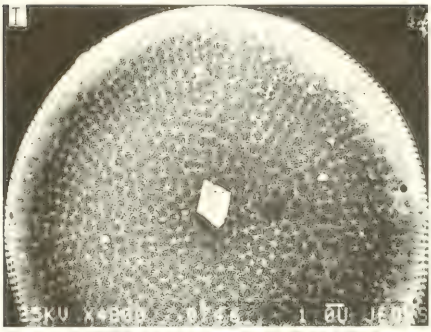
FIGURES 7–10. SEM. *Actinocyclus trapeziformis* (with varieties), specimens from the Upper Oligocene sediments of West Siberia. FIGURE 7. Detail of the external valve surface with a distinct hyaline ring on the boundary of the valve face and mantle with irregularly located solid conic spines. FIGURE 8. External valve surface with the marginal ring of rimoportulae openings on the mantle. FIGURE 9. External valve surface with distinct areolae fascicles. FIGURE 10. Internal valve surface with a pseudonodulus and marginal ring of rimoportulae. FIGURES 11–13. SEM. *Actinocyclus lobatus*, specimens from the Lower Miocene sediments of West Siberia. FIGURE 11. External valve surface with a single pseudonodulus and lobed spines located along the external rim of the hyaline ring on the valve face-mantle junction. FIGURE 12. Detail of the external valve mantle surface with one lobed spine, a pseudonodulus and rimoportula opening in the base of narrow hyaline strip. FIGURE 13. Detail of the internal valve mantle surface with one rimoportula having the shoe-shaped slit extension in the apical part.

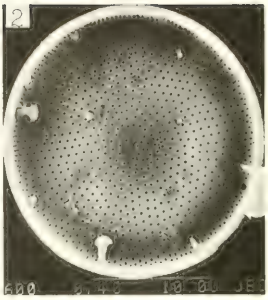
Plate 3, Figures 14–19

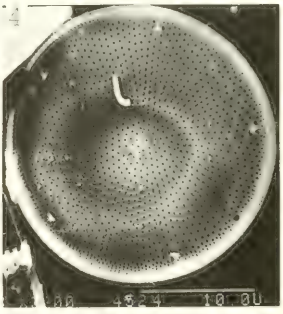
FIGURES 14–16, 19. SEM. *Undatodiscus variabilis*, specimens from the Upper Miocene sediments of West Kamchatka. FIGURE 14. Detail of the external valve surface with three dome-like convexities in the periphery. FIGURE 15. Internal valve surface with concavities on the periphery in which rimoportulae are placed. FIGURE 16. Detail of the internal valve surface with a pseudonodulus and two rimoportulae located in concavities. FIGURE 19. Detail of the internal valve surface with the rosette of areolae in the center and the marginal ring of rimoportulae in concavities. FIGURES 17, 18. SEM. *Undatodiscus tubiformis*, specimens from the Lower Miocene sediments of West Siberia. FIGURE 17. Detail of the external valve surface with arolae cribra and a thin-wall, trapezium-like process penetrated by the rimoportula tube. FIGURE 18. Structure of the external valve surface.

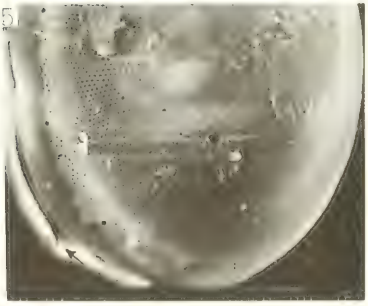
Plate 4, Figures 20–25

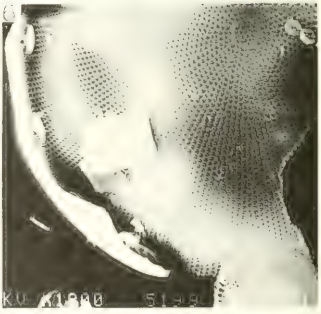
FIGURES 20–25. SEM. *Lobodiscus sibiricus*, specimens from the Middle-Upper Miocene sediments of the Tunkin hollow. FIGURE 20. Detail of the external valve surface with areolae cribra. FIGURE 21. Detail of the internal valve surface with a pseudonodulus. FIGURE 22. Detail of the external valve surface with an unbroken cribrum of areolae and the lobed spine. FIGURE 23. Detail of the valve mantle with the internal part of rimoportula and its external opening on the distal rim of the lobed spine with the ultrastructure. FIGURE 24. Detail of the valve mantle with half-closed areolae (both with the external cribrum and the internal domed velum) located in two layers, as well as with fragments of rimoportulae and lobed spines. FIGURE 25. Detail of the valve mantle with a short external tube of rimoportula evident directly under the lobed spine.

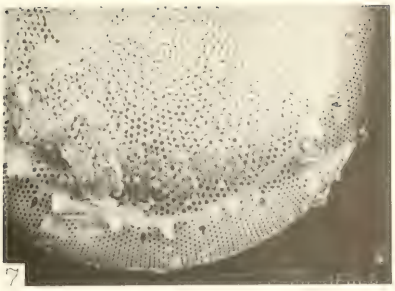


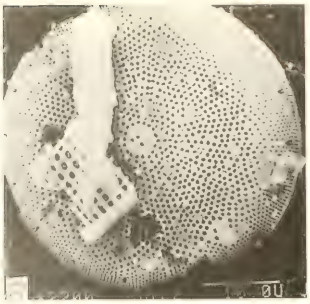


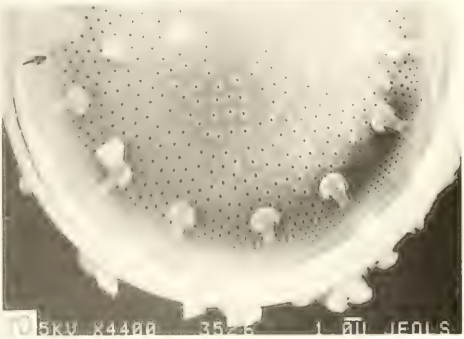


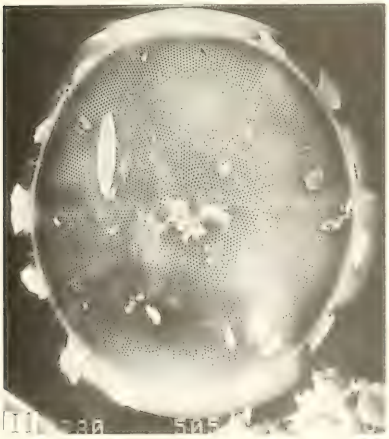


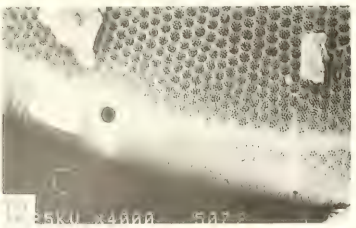


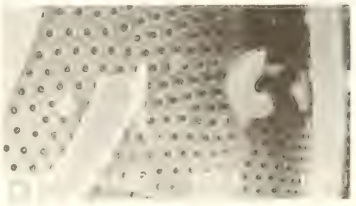






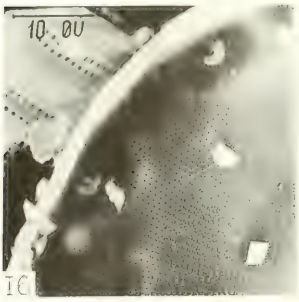


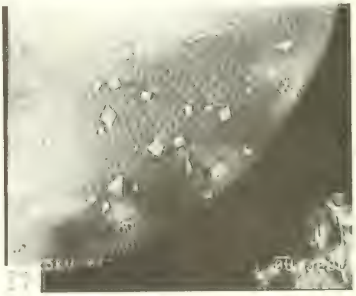


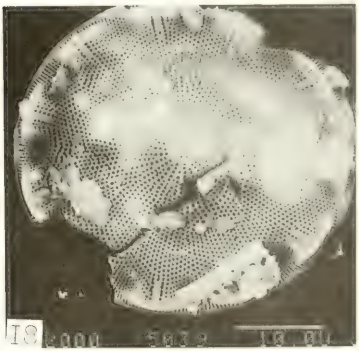


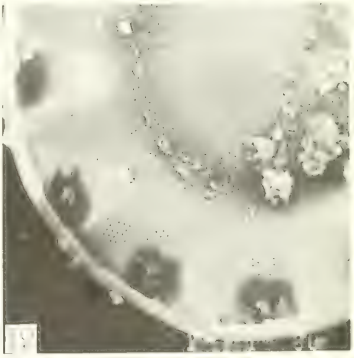
I4
10.0U

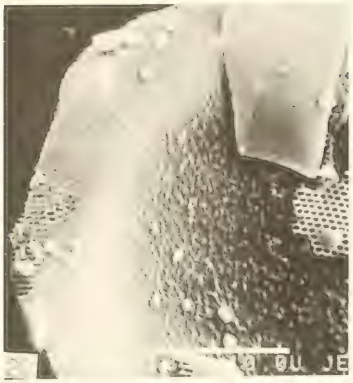
I5
10.0U

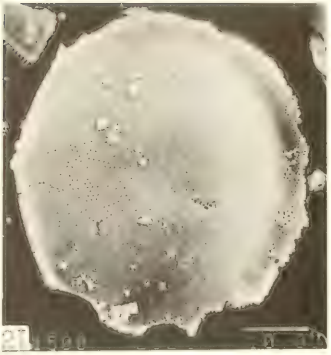

10.0U
I6

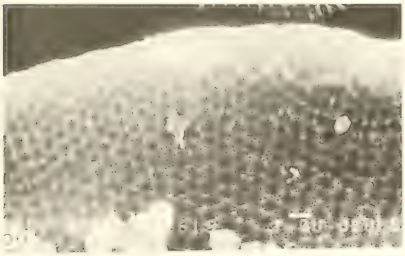

I7


I8


I9







Morphology and Taxonomy of Some Centric Diatom Species From the Miocene Sediments of the Dzhilinda and Tunkin Hollows

by

Galina K. Khursevich

Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Zhodinskaya Street 7, 220600 Minsk, Byelorussia

with 4 plates

Abstract: Valve ultrastructure of dominant, biostratigraphically valuable diatom species from the Miocene freshwater sediments of the Dzhilinda and Tunkin hollows was studied with scanning electron microscopy (SEM). Five new taxa—*Alveolophora tscheremissionovae* sp. nov., *Aulacoseira robusta* sp. nov., *Ellerbeckia kochii* var. *antiqua* var. nov., *Stephanodiscus dzhilindus* sp. nov., and *Actinocyclus tunkaensis* sp. nov.—are described and compared to congeners. The stratigraphic distribution of these extinct species is presented.

Introduction

Detailed study of diatom assemblages from the Neogene deposits of the Dzhilinda and Tunkin hollows, located east and southwest of Lake Baikal, respectively, was carried out under the light microscope (LM) by Tscheremissinova (Endrikhinsky and Tscheremissinova 1970; Tscheremissinova 1973). She determined a fairly rich planktonic diatom complex with various *Melosira* and *Coscinodiscus* species. Later, the great majority of known freshwater *Melosira* species was transferred to the genus *Aulacosira* Thw. (Simonsen 1979; Moisseeva 1981), and one, *M. jouseana* Moiss., was transferred into the new genus *Alveolophora* Moiss. & Nevretd. (Moisseeva and Nevretdinova 1990). *Melosira scabrosa* Ostr., now considered a synonym of *M. teres* Brun (Evans 1964; Moisseeva and Genkal 1987), has been transferred to the genus *Ellerbeckia* Crawford (Crawford 1988). Freshwater species of *Coscinodiscus* from the Miocene sediments of different regions of the northern hemisphere have recently been transferred to the genus *Actinocyclus* Ehrenberg (Bradbury 1984; Bradbury et al. 1985; Khursevich et al. 1990; Rubina and Khursevich 1990), based on SEM observations. An exception is an extinct species, *Coscinodiscus lobatus* var. *sibericus* Tscher. (Tschremissinova 1971:54–56, Pl. I, Figs. 7–9), from the Middle-Upper Miocene sediments of the Tunkin hollow, whose ultrastructural features have permitted it to be distinguished as a new genus of freshwater diatoms, *Lobodiscus* Lupik. & Churs. (Lupikina and Khursevich, in press). Preliminary electron-microscopic

observations of numerous diatom valves of the genera *Melosira* Ag. *sensu lato* and *Coscinodiscus* Ehrenberg, served as a basis for the present report. Morphological peculiarities observed in these groups suggest the description of several new species and a new variety.

Materials and Methods

The terminology proposed by Ross et al. (1979) and in the book *Diatom Algae of the USSR (Fossil and Recent)* (1988) is used. For LM, samples were processed using methods generally accepted in the former U.S.S.R, and observed with a Zeiss-Jena Amplival. For SEM, specimens were sputter coated with gold and observed with a JEOL-35C.

Description of Species

Alveolophora tscheremissinovae sp. nov.
(Figs. 1, 2, 5–9)

SYNONYM: Melosira praedistans Jousé sensu Tscheremissinova, 1971:54, Pl. I, Figs. 3, 4; 1975:25, Pl. I, Figs. 11, 12.

DESCRIPTION: Frustules short cylindrical and linked into long or short chains by interlocking spines. Valves 10–24 µm in diameter, 1.2–2.5 µm in height; pseudosepta and pseudoalveolae poorly developed in periphery of valves. External surface of the disk covered by granules. Areolae with external rotae and internal cribra, which are poorly preserved in fossil taxa, in submarginal zone of the disk in radial rows, 8–12 in 10 µm; in the valve center areolae are irregularly arranged or absent. Radial areolar rows in narrow (2–5 rows) or broad (6–11 rows) sectors separated by straight or curved hyaline strips, transformed into pseudosepta on internal surface of valve mantle. Rimoportulae (4–12 on the valve) form a ring in the submarginal zone of the disk. Internally they are represented by small hillocks perforated by a slit; externally they appear as small openings. Pattern of areolae on mantle usually in straight vertical rows; 8–12 rows in 10 µm, with 2–3 patterns in each. Short spatulate interlocking spines on valve face-mantle junction.

HOLOTYPE: N 2/437-T.h. in the collection of the Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Minsk.

TYPE LOCALITY: The Baikal area, the Tunkin hollow, the borehole 2, depth 111 m, the Tankhoi suite, the Middle-Upper Miocene, in the mass.

COMMENTS: This species occurs in the Vitim plateau, Dzhilinda suite of the Lower-Middle Miocene also. It differs from other representatives of the genus *Alveolophora* (Moisseeva and Nevretdinova 1990) mainly by a poor development of pseudosepta and pseudoalveolae in the valve periphery and by the location of rimoportulae on the surface of the valve face.

Aulacosira robusta sp. nov.
(Figs. 11–13)

DESCRIPTION: Frustules short cylindrical, united by interlocking spines in more or less long filaments. Valves faintly radially undulate on periphery of valve face. Generally wider than long, 17–23 µm in diameter, 3–5 µm high. Structure of mantle consists of oblique rows of 4–5 coarse and widely spaced areolae, forming 10–12 striae in 10 µm. They are separated by interstriae (8–10 in 10 µm); some are rib-like. One or two rows of similarly coarse areolae occur on periphery of valve face, lying between spines and in line with mantle areolae rows. A short bulbous spine inserts from each interstria on the valve face-mantle junction. Ring of siliceous markings are present in the submarginal

zone of the disk in some specimens. Both spines and these markings serve to link valves. Pseudoseptum very deep and obvious. Rimoportulae not observed. Some specimens with a very thin basal siliceous layer at central part of the valve as compared with periphery.

HOLOTYPE: N 210-D.h. in the collection of the Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Minsk.

TYPE LOCALITY: Vitim plateau, the Dzhilinda hollow, outcrop on the right bank of the Dzhilinda river lower stream; the Dzhilinda suite, the Lower-Middle Miocene, in the mass.

COMMENTS: The species is very close to *A. lirata* (Ehrenberg) Ross (Haworth 1988:141, Figs. 16–19) but it differs by the larger diameter of valves, more shallow mantle, and different form of spines (*A. lirata* has cruciform spines; diameter of valves 7–16 µm, height 7–10 µm). The observation of lightly silicified valve centers and thick edges suggests valve ontogeny in *Aulacosira* originates at the periphery and progresses to the valve center.

Ellerbeckia kochii var. *antiqua* var. nov.
(Figs. 17–22)

DESCRIPTION: Cells tightly united by linking structures on valve faces to form long chains. Frustule broadly cylindrical, complex. Valves 35–80 µm in diameter, 17–22 µm in height. Linking structures of relief valve represented by short radial ridges (8–9 in 10 µm) in the submarginal zone of the valve face, and corresponding structures of intaglio valve are radial grooves. Remainder of the valve face is unstructured. Externally, relief valve with stepped mantle concave; intaglio valve with plain mantle convex. Valve mantle penetrated by pores, 20–22 in 10 µm of the vertical row. Vertical rows of pores (24–30 in 10 µm) separated by narrow ribs. Original tube processes (2–3 in 10 µm) formed by 6–8 ribs curved spirally upwards and alternate with pores on internal surface of valve mantle. Externally tube- processes terminate by openings. They are located irregularly in 2–3 rings. Mantle edge crenulate. Crenulations interdigitate with similar structures on valvocopula. Valvocopula consists of thin pores: 42–44 pores in 10 µm of vertical rows, 44–46 pores in 10 µm of horizontal rows. Valves of a frustule united by means of a circular interlocking diaphragm, located along the mantle rim in valvar plane. Diaphragm relief represented by a system of alternating shallow radial furrows and ribs.

HOLOTYPE: N 202-D.h. in the collection of the Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Minsk.

TYPE LOCALITY: Vitim plateau, the Dzhilinda hollow, outcrop on the right bank of the Dzhilinda river lower stream; the Dzhilinda suite, the Lower-Middle Miocene, in the mass.

COMMENTS: The new variety differs from *Paralia* (= *Ellerbeckia*) *kochii* (Pant.) Moiss. (Moisseeva and Genkal 1987:1502–1503, Pl. II; see Temniskova-Topalova et al. this volume for new combination of *E. kochii*) in the structure of the tube processes. It resembles *E. arenaria* (Moore ex Ralfs) Crawford in possessing crenulations on the mantle edge (Crawford 1988), but differs by having a circular linking diaphragm (Moisseeva and Genkal 1987) that helps to join valves within a frustule.

Stephanodiscus dzhilindus sp. nov.
(Figs. 3, 4, 14–16)

DESCRIPTION: Frustule discoid. Valves with a slightly concave center, 5.2–10 µm in diameter. Areolae 10–12 in 10 µm, located in uniseriate, radial striae separated by ribs, 8–10 in 10 µm. A single fultoportula with two struts resides on valve face. One rimoportula occurs on the boundary of the valve face and mantle. Valve mantle is low (up to 1.2 µm

in height) with 2–3 areolae in a vertical row and with 30–40 areolar rows in 10 μm. Fultoportulae with three struts, placed on each second rib under a spine.

HOLOTYPE: N 194-D.h. in the collection of the Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Minsk.

TYPE LOCALITY: Vitim plateau, the Dzhilinda hollow, outcrop on the right bank of the Dzhilinda river lower stream; the Dzhilinda suite, the Lower-Middle Miocene, in the mass.

COMMENTS: *Stephanodiscus dzhilindus* differs from the small species *Stephanodiscus parvus* Stoermer & Håkansson (Stoermer and Håkansson 1984:305–306, Figs. 1–11) by a coarse areolation of the valve surface (*S. parvus* has 25–30 areolae in 10 μm along the radius of the valve) as well as by the higher density of fultoportulae on the valve mantle.

Actinocyclus tunkaensis sp. nov.
(Figs. 10, 23–28)

SYNONYM: Coscinodiscus gorbunovii var. ethmodiscoides Moiss. sensu Tscheremissinova 1973: Pl. III, Figs. 11–13; Pl. VI, Figs. 1–4.

DESCRIPTION: Frustule short, cylindrical, 26–60 μm in diameter. Cingulum composed of closed bands; valvocopula wide and hyaline. Valves circular, strongly concentrically undulate, with one or two distinct convex and concave zones. Central area small, with 1–4 isolated areolae or not developed. Areolae loculate with criba on the external valve surface and foramina on the interior, arranged in radial rows, 8–14 in 10 μm. Size of areolae and their density differ between the central, middle, and submarginal zones of the valve face. Areolae are denser (14–16 in μm) in the central and submarginal zones than in the middle (6–10 areolae in 10 μm) on valves with a concave center. Areolae are more widely spaced (8–10 in 10 μm) in the central and submarginal zones than in the middle one (12–14 areolae in 10 μm) on valves with a convex center. Hyaline ring usually present on valve face-mantle junction. Valve mantle from 3.1 to 5.3 μm high, with 6–10 small areolae in a vertical row and 20–26 areolar rows in 10 μm. Marginal ring of rimoportulae (their number varies from 6 to 12) located in the base of short hyaline strips near the upper boundary of the mantle. Internally rimoportulae have short, broad tubes with fan-shaped ends; externally they terminate by openings. Pseudonodulus not observed on any valves.

HOLOTYPE: N 2/440-T.h. in the collection of the Institute of Geochemistry and Geophysics, Byelorussian Academy of Sciences, Minsk.

TYPE LOCALITY: Baikal area, the Tunkin hollow, borehole 2, depth 66.2 m; the Tankhoi suite, the Middle-Upper Miocene, in the mass.

COMMENTS: This species differs from all known taxa of *Actinocyclus* by the constant absence of a pseudonodulus as well as by the above-characterized relief and structure of the valve face surface.

Discussion

It is interesting to note that the diatom taxa described here are all extinct.

Many investigators (Crawford 1979, 1988; Simonsen 1979; Moisseeva and Nevretdinova 1990; Lupikina and Khursevich 1991) repeatedly have expressed an opinion on the heterogeneity of the genus *Melosira sensu lato*. A detailed survey of the literature on the freshwater species of *Melosira s. l.* leads to the conclusion that within the broad concept of the genus, six independent genera may be recognized: *Aulacosira*, *Alveolophora*, *El-*

lerbeckia, *Melosira s. str.*, *Orthosira* Thw., and *Pseudoaulacosira* Lupik. & Churs. The genera *Alveolophora* and *Pseudoaulacosira* were first revealed from the Upper Cenozoic sediments of the former U.S.S.R. (Moisseeva and Nevretdinova 1990; Lupikina and Khursevich 1991), and five *Alveolophora* taxa have been found in the former Soviet Union.

Melosira sp. aff. *M. jouseana* Moiss., has been reported from Upper Miocene sediments of the western Snake River basin, U.S.A. (Bradbury and Krebs 1982: Pl. XII), and, as *Melosira* aff. *jouseana* Moiss., from the Lower-Middle Miocene lacustrine deposits of Turkey (Servant-Vildary et al. 1988:166–167, Figs. 3–19). These specimens may also be related to *Alveolophora* species due to the presence of pseudosepta and pseudoalveolae on the internal surface of the mantle. However, the American species has a different type of areolae velum (in particular, the external sinked vola with attached cribrum) and the location of rimoportulae on the internal surface of pseudoseptum differs from *Alveolophora tscheremissinovae*. The Turkish species is characterized by different valve shapes (from trilobate to sub-circular) and the presence of internal rota in the areolae. The location of rimoportulae could not be observed.

Along with *A. tscheremissinovae*, the extinct species *Pseudoaulacosira moisseevae* (Lupik.) Lupik. & Churs. (unknown outside the former U.S.S.R.) was distributed in Miocene deposits of Siberia and the Far East. It differs from the genus *Aulacosira* Thw. by the development of a two-sided velum in the areolae of the disk (the internal cribrum and the external slightly sinked rota), narrow radial ribs in the periphery of the valve, and small markings in the middle part of the external disk surface, which apparently help to link valves (Lupikina and Khursevich 1991).

Stephanodiscus species are few in continental Miocene sediments. Therefore, the discovery of *S. dzhilindus* in the Lower-Middle Miocene deposits of the Vitim plateau (dated by the K-Ar method) represents an important find of the genus *Stephanodiscus* Ehrenberg relative to its evolution in the Neogene. The material shows that *Stephanodiscus* and *Cyclostephanos* species appeared on the territory of the former U.S.S.R. earlier (in the Early-Middle Miocene) than representatives of the genus *Cyclotella* (Khursevich 1989). *Cyclotella* and *Stephanodiscus* species are known in the Neogene freshwater sediments of the United States and Africa, mainly from the Upper Miocene (Krebs et al. 1987; Fourtanier and Gasse 1988).

Acknowledgements

I am grateful to E. A. Tscheremissinova and hab. N. N. Lavrenko for providing material from diatom collections on the Tunkin and Dzhilinda hollows. I would like to thank to S. A. Fedenya for all the kind of technical help. My sincere thanks are due to A. I. Moisseeva and E. G. Lupikina for discussion on the frustule morphology of new taxa.

Literature Cited

BRADBURY, J. P. 1984. Fossil *Actinocyclus* species from freshwater Miocene deposits in China and the United States. Pp. 157–171 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

BRADBURY, J. P., K. V. DIETERICH, AND J. L. WILLIAMS. 1985. Diatom flora of the Miocene lake beds near Clarkia in northern Idaho. Late Cenozoic History of the Pacific Northwest: Pac. Div. Am. Assoc. Adv. Sci. 33–59.

BRADBURY, J. P. AND W. N. KREBS. 1982. Neogene and Quaternary lacustrine diatoms of the western Snake river basin, Idaho-Oregon, U. S. A. Acta Geol. Acad. Sci. Hungaricae 25:97–122.

CRAWFORD, R. M. 1979. Filament formation in the genera *Melosira* C.A. Agardh and *Paralia* Heiberg. Nova Hedwigia, Beih. 64:121– 133.

———. 1988. A reconsideration of *Melosira arenaria* and *M. teres*; resulting in a proposed new genus *Ellerbeckia*. Pp. 413– 433 *in* Algae and the Aquatic Environment, F. E. Round, ed. Biopress Ltd., Bristol.

DIATOM ALGAE OF THE USSR (FOSSIL AND RECENT). 1988. Vol. 2 (1). Leningrad, Nauka, 116 pp.

ENDRIKHINSKY, A. S. AND E. A. TSCHEREMISSINOVA. 1970. O nakhozhdenii miozenovykh otlozheny na Vitimskom ploskogorie. Doklady AN SSSR 191:885–888.

EVANS, G. H. 1964. The fossil diatoms from lake deposits of the English Lake District. New Phytol. 63:413–417.

FOURTANIER, E. AND F. GASSE. 1988. Premiers jalons d'une biostratigraphie et evolution des diatomées lacustres d'Afrique depuis 11 M. a. C. R. Acad. Sci. Paris, 306, Serie II:1401–1408.

HAWORTH, E. Y. 1988. Distribution of diatom taxa of the old genus *Melosira* (now mainly *Aulacosira*) in Cumbrian waters. Pp. 138–167 *in* Algae and the Aquatic Environment, F. E. Round, ed. Biopress Ltd., Bristol.

KHURSEVICH, G. K. 1989. Atlas vidov *Stephanodiscus* i *Cyclostephanos* (Bacillariophyta) iz verkhnekainozoiskikh otlozheny SSSR. Minsk, Nauka i tekhnika, 167 p.

KHURSEVICH, G. K., A. I. MOISSEEVA, T. F. KOZYRENKO, AND N. V. RUBINA. 1990. New taxa of the genus *Actinocyclus* (Bacillariophyta) from the Neogene freshwater sediments of the U. S. S. R. Bot. Zh. 75:1439–1442.

KREBS, W. N., J. P. BRADBURY, AND E. THERIOT. 1987. Neogene and Quaternary lacustrine diatom biochronology, Western U.S.A. Palaios, Vol. 2, 505–513.

LUPIKINA, E. G. AND G. K. KHURSEVICH. 1991. *Pseudoaulacosira*—a new genus of freshwater diatoms in the class Centrophyceae. Bot. Zh. 76:290–291.

——. In press. *Lobodiscaceae*—novoe semeistvo diatomovykh vodoroslei klassa Centrophyceae. Paleontologichesky Zhurnal.

MOISSEEVA, A. I. 1981. Revizia sistematicheskogo polozhenia presnovodnykh vidov roda *Melosira* Ag. (Bacillariophyta). Sistematika, evoluzia, ekologia vodorslei i ikh znachenie v praktike geologicheskikh issledovany. Kiev, Naukova dumka, 124–126.

MOISSEEVA, A. I. AND S. I. GENKAL. 1987. On freshwater species of the genus *Paralia* (Bacillariophyta). Bot. Zh. 72:1500–1504.

MOISSEEVA, A. I. AND T. L. NEVRETDINOVA. 1990. The new family and genus of freshwater diatom algae (Bacillariophyta). Bot. Zh. 75:539–544.

RADIONOVA, E. P. 1987. Morfologia diatomei roda *Cestodiscus* iz nizhne-srednemiozenovykh otlozheny tropicheskoizony Tikhogo okeana. Voprosy mikropalentologii. Vyp. 29:141–154.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An emended terminology for siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

RUBINA, N. V. AND G. K. KHURSEVICH. 1990. New representatives of the genus *Actinocyclus* (Bacillariophyta) from the Late Oligocene of West Siberia. Bot. Zh. 75:1565–1567.

SERVANT-VILDARY, S., J. C. PAICHELER, AND B. SEMELIN. 1988. Miocene lacustrine diatoms from Turkey. Pp. 165–180 *in* Proceedings of the 9th International Diatom Symposium, F. E. Round, ed. BioPress, Ltd, Bristol and O. Koeltz, Koenigstein.

SIMONSEN, R. 1979. The diatom system: ideas on phylogeny. Bacillaria 2:9–71.

STOERMER, E. F. AND H. HAKANSSON. 1984. *Stephanodiscus parvus*: validation of an enigmatic and widely misconstrued taxon. Nova Hedwigia, Beih. 39:497–511.

TSCHEREMISSINOVA, E. A. 1971. Novye i interesnye vidy diatomovykh vodoroslei iz neogena Pribaikaliaa. Nov. Syst. Plant. Non-Vasc. 8:52–66.

———. 1973. Diatomovaya flora neogenovykh otlozheny Pribaikalia. Novosibirsk, Nauka, 68 pp.

Explanation of Plates

Plate 1, Figures 1–10

FIGURES 1, 2, 5–9. *Alveolophora tscheremissinovae*, specimens from the Middle-Upper Miocene sediments of the Tunkin hollow. FIGURE 1. SEM. External view showing the structure of the valve face. FIGURES 2, 5, 6, 9. SEM. Internal views showing pseudosepta and pseudoalveolae on the valve mantle and the ring of rimoportulae in the submarginal zone of the disk. FIGURES 7, 8. LM. Valve view. FIGURES 3, 4. LM. *Stephanodiscus dzhilindus*, specimens from the Lower-Middle Miocene sediments of the Dzhilinda hollow. Valve view. FIGURE 10. LM. *Actinocyclus tunkaensis*, specimen from the Middle-Upper Miocene sediments of the Tunkin hollow. Valve view.

Plate 2, Figures 11–16

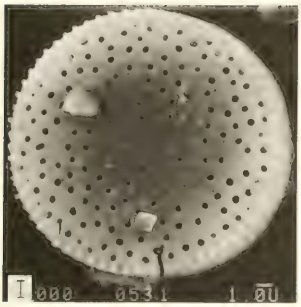
FIGURES 11–13. SEM. *Aulacosira robusta*, specimens from the Lower-Middle Miocene sediments of the Dzhilinda hollow. FIGURE 11. Chain consisting of two and one-half frustules. FIGURE 12. External valve face with one concentric row of areolae and the ring of simple markings (arrow) on the periphery. FIGURES 14-16. SEM. *Stephanodiscus dzhilindus*, specimens from the Lower-Middle Miocene sediments of the Dzhilinda hollow. FIGURE 14. External view showing the areolate structure of the valve face and the external opening of the fultoportula (arrow). FIGURE 15. External view showing the areolate structure of the valve face and mantle. FIGURE 16. Internal view with a single fultoportula with two struts near the center of the valve face, one rimoportula (arrow), and the marginal ring of fultoportulae with three struts on the valve mantle.

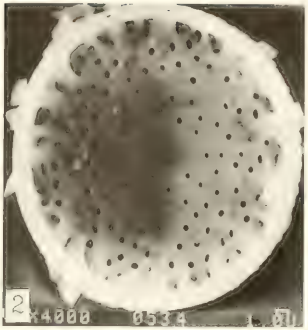
Plate 3, Figures 17–22

FIGURES 17–22. SEM. *Ellerbeckia kochii* var. *antiqua*, specimens from the Lower-Middle Miocene sediments of the Dzhilinda hollow. FIGURE 17. Structure of the relief valve with stepped mantle and valvocopula in girdle view. FIGURE 18. Structure of the external frustule surface in girdle view. FIGURE 19. Detail of the valve mantle–valvocopula junction. FIGURE 20. Structure of the intaglio valve with plain mantle. FIGURE 21. Detail of the internal valve surface with tube processes and the circular interlocking diaphragm located along the mantle rim in valvar plane (arrow). FIGURE 22. Structure of tube processes on the internal valve mantle.

Plate 4, Figures 23–28

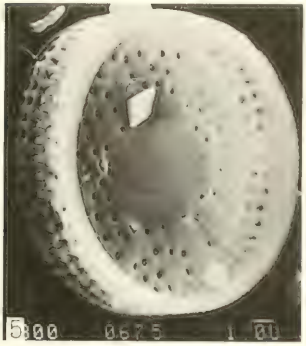
FIGURES 23–28. SEM. *Actinocyclus tunkaensis*, specimens from the Middle-Upper Miocene sediments of the Tunkin hollow. FIGURE 23. Structure of the valve surface with the marginal ring of rimoportulae external openings on the mantle (arrow). FIGURE 24. Structure of the external valve surface with the different density of areolae arrangement in the central, middle, and submarginal parts of the valve face and on the mantle. FIGURE 25. Detail of the external valve surface with external cribra of areolae. FIGURE 26. Structure of the external surface of valves with the concave and convex centers. FIGURE 27. Detail of the internal valve surface with foramina of loculate areolae. FIGURE 28. Structure of the internal valve surface with marginal ring of rimoportulae on the mantle.


1
1 0U


2

3

4
10 0U


5
1 0U

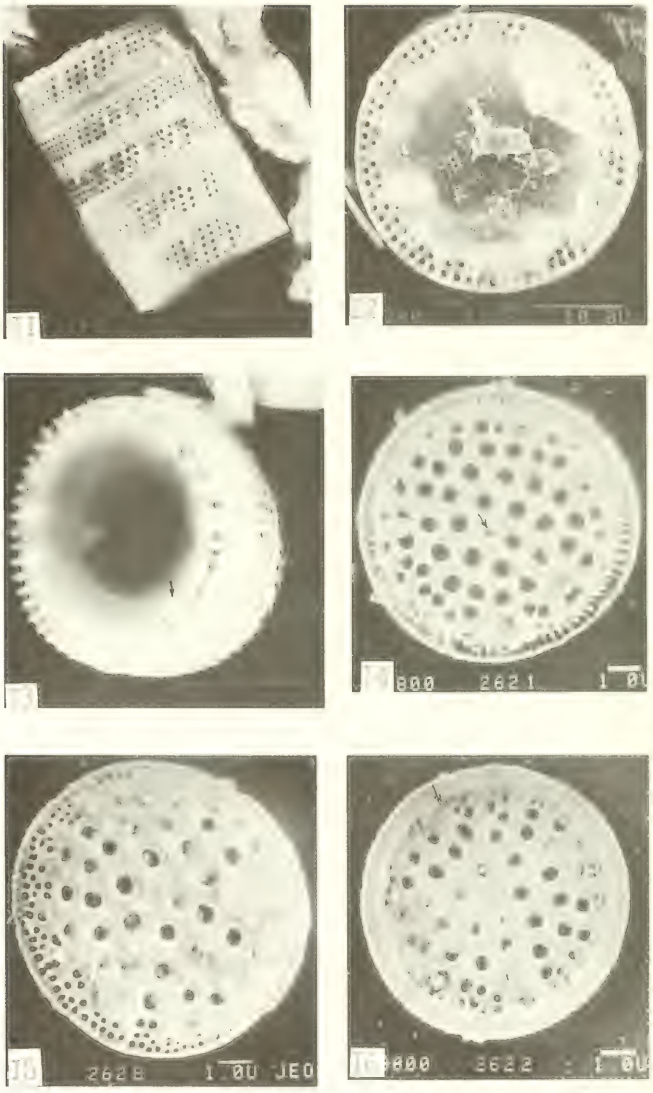
6
10 0U

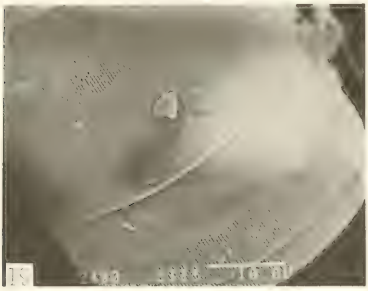
7
10 0U

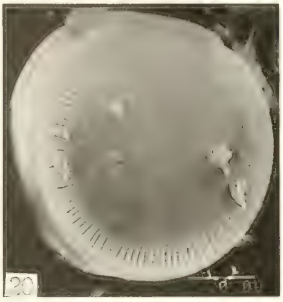
8
10 0U

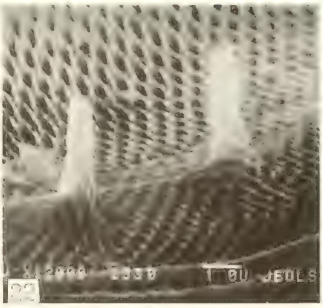
9

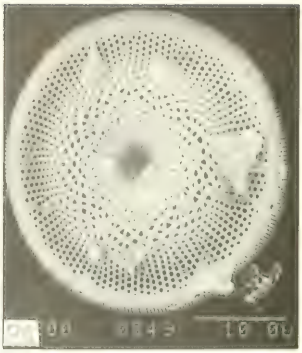
10
10 0U

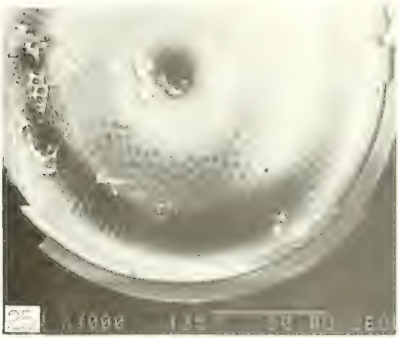

800 2621
2628 1 0U JEO

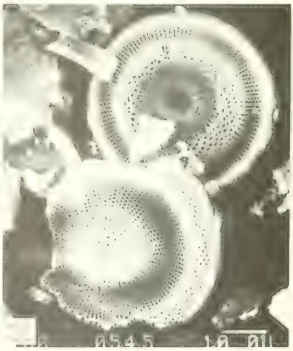


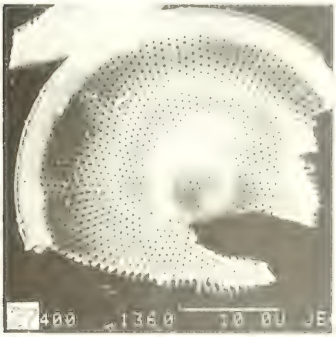












Taxonomy and Morphology of Two Forms of the *Nitzschia sinuata* Complex

by

Hiromu Kobayasi, Shinji Kobori, and Satoshi Sunaga

Tokyo Diatom Institute, Honcho 3-8-9-813,
Koganei-shi, Tokyo 184, Japan

with 4 plates

Abstract: Fine structure of taxa previously identified as *Nitzschia sinuata* var. *tabellaria* (Grun.) Grun. and *N. sinuata* var. *delognei* Lange-Bertalot were examined with SEM and TEM and compared with the nominate variety. Differences in areolar occlusions and valve shape in transapical section were observed. These observations led to the conclusion that not only are these taxa independent of *N. sinuata* var. *sinuata* but also of each other. The correct names of *N. sinuata* var. *tabellaria* and *N. sinuata* var. *delognei* are *N. tabellaria* (Grun.) Grun. and *N. solgensis* Cleve-Euler, respectively.

Introduction

Nitzschia tabellaria (Grun.) Grun. was first described as an independent species of the genus *Denticula* by Grunow (1862), and was transferred to the genus *Nitzschia* in 1880 (in Cleve and Grunow 1880). Grunow later (in Van Heurck 1881) treated this taxon as a variety of *N. sinuata* (Thwaites ex W. Smith) Grun. This status has been accepted by many authors based presumably on its sinuous outline and prominent central inflation (Krammer and Lange-Bertalot 1986).

The diatom known as *Nitzschia solgensis* Cleve-Euler was first described by Grunow (in Van Heurck 1881) as a variety of *N. denticula* under the name "var. *delognei*." It was transferred to a variety of *N. sinuata* by Lange-Bertalot (1988). Cleve-Euler (1952) recognized this taxon as an independent species and gave it the name *N. solgensis*, since the name *N. delognei* Grun. (in Van Heurck 1885) existed as an earlier homonym.

In the present paper, the fine structure of these two diatoms ascribed to the *N. sinuata* complex are compared with that of *N. sinuata* var. *sinuata*, in order to elucidate their systematic relationships.

Materials and Methods

Materials used in this study are listed under the appropriate species. Materials were gently boiled in concentrated sulfuric acid for 30 minutes. After several washes in distilled water, a drop containing diatoms was placed on a formvar-coated grid for TEM or on a cover glass, followed by coating with gold-palladium, for SEM. JEOL 100CX-II (TEM) and

JEOL F15 (SEM) microscopes were used in the examination.

Results and Discussion

Nitzschia tabellaria (Grun.) Grun. in Cleve et Grunow 1880, p. 82.

BASIONYM: *Denticula tabellaria* Grun. 1862, p. 548, Pl. 12, Figs. 26a–e.

SYNONYM: *Nitzschia sinuata* var. *tabellaria* (Grun.) Grunow in Van Heurck 1881, Pl. 60, Figs. 12, 13.

STUDY MATERIALS: Scrapings from a boulder on the river bed of the Kanna-gawa (Kanna River) just beneath Shimokubo Dam, Gunma Pref., on 23 Feb. 1975, WT. 4° C, pH 8.3, coll. H. Tanaka, K-2129; Kanna-gawa (Kanna River) just beneath Shimokubo Dam, Gunma Pref., on 6 Nov. 1987, coll. S. Ishii, K-6643; Epiphytic on aquatic plants of Unagi-ike (Unagi Pond) in Kagoshima Pref. on 11 Feb. 1984, WT. 9° C, pH 8.0, K-1792. Comparative material of *N. sinuata*: Gray/brown jelly covering the wet rock-face on the bank of a canal at Llangollen in North Wales on 19 Apr. 1976, coll. B. Hartley, K-6462.

This small and characteristic species with a central inflation of the valve is widely distributed in Japan in both running and stagnant waters. Valves are 8.5–21 µm long, 4–7.5 µm wide (Figs. 1–4).

In the SEM, the valve face is longitudinally undulate. The raphe is borne on the top of the elevated raphe canal, and distal from the raphe there is an inward trough in the valve. This species resembles *Denticula tenuis* Kütz. rather than *N. sinuata* in having a longitudinally undulated valve and a smoothly curved face/mantle juncture without the marginal ridge (Figs. 5, 6) (Mann 1978). The raphe is continuous from pole to pole and ends in fishhook-shaped terminal fissures. Both terminal fissures of a single valve curve in the same direction, towards the distal margin (Fig. 6), but they may sometimes curve towards the proximal margin (Fig. 9, arrow). Areolae are closed by a hymen with perforations arranged in a hexagonal array (Fig. 8). In *N. sinuata* (Figs. 11, 12) the areolae are also closed by a hymen with the same arrangement of perforations, but the hymen is overlaid with the cribrum (Fig. 13) (see also Mann 1981, Fig. 8). The cingulum is composed usually of four open bands, including a broad valvocopula, two narrow bands, and a broad final band. The first wide band bears a single transverse row of poroids at the junction between the pars interior and the pars exterior. The second and third bands are similar to one another and are unperforated. The fourth band is the widest and bears a transverse row of longitudinally elongated poroids. Only the first and second bands bear numerous warts on the pars exterior (Figs. 9, 10).

Though this species has a number of features in common with *N. sinuata*, the differences in the areolar occlusions and shape of the face/mantle junction appear to be sufficient enough to warrant it as an independent species.

Nitzschia solgensis Cleve-Euler 1952, p. 67, Figs. 1451c, d.

SYNONYMS: *Nitzschia denticula* var. *delognei* Grun. in Van Heurck 1881, Pl. 60, Fig. 9. *Nitzschia sinuata* var. *delognei* (Grun.) Lange-Bertalot 1988, p. 54, Figs. 83–86, nec Figs. 77–82.

STUDY MATERIALS: Damp moss on a stream-side rock at Shiozawa- rindou (Shiozawa Logging Road), one of the uppermost branchlets of the Kanna-gawa (Kanna River), Gunma Pref., Central Japan, on 20 Aug. 1982, coll. H. Tanaka, K-2153; comparative material of *N. heidenii* (Meister) Hustedt; bottom mud of a small pond in the Koishikawa Botanical Garden, Tokyo, on 15 Jul. 1987, coll. Nagumo of the Nippon Dental University, N-1199.

Valves of this species are small and linear-lanceolate in shape, 12–25 μm long and 3–5 μm wide (Figs. 16–19). Fibulae are 5–7 in 10 μm and striae number 22–26 in 10 μm. These values of size and fibulae and striae densities are identical to those reported from type material by Lange-Bertalot (1980).

In the SEM the valve is sharply angled at the raphe canal so that the proximal mantle is higher/broader than the distal mantle. The proximal mantle bears areolae, but they are lacking on the distal mantle. There is a prominent marginal ridge on the well-defined distal mantle (Figs. 20, 23, 24). Although there is no marginal ridge in the figure presented by Mann (1984, Fig. 2g), such a ridge does seem to be present in a previous figure of his (Mann 1978, Fig. 800). The structure of the raphe and fibulae and the arrangement of areolae are identical to those in both *N. sinuata* and *N. tabellaria*. Areolae are, however, closed by a hymen with perforations arranged in a hexagonal array as was seen in *N. tabellaria* (Figs. 27, 28).

The cingulum is composed usually of four open bands, which include a broad valvocopula, two narrow bands, and the broadest, final band. The first band bears a single transverse row of poroids at the junction between the pars interior and the pars exterior and has numerous warts on the pars exterior. The second and third bands are unperforated and similar to one another, but the second has a row of small warts on its abvalvar edge. The fourth band bears a transverse row of longitudinally elongate poroids (Figs. 24–26).

Though this taxon has nearly the same dimensional features as *N. tabellaria*, the more eccentric raphe canal and the smooth distal edge with a marginal ridge seem to be sufficient to warrant recognition of this taxon as an independent species. Mann (1978) once treated this taxon as an independent species, but later (1984) applied the name *N. sinuata* var. *delognei* to it.

When Lange-Bertalot (1980) suggested that *N. solgensis* may be more closely allied to *N. sinuata* than *N. denticula*, and proposed the combination *N. sinuata* var. *delognei*, he extended the circumscription of this variety to include *N. heidenii* and *N. interrupta* (Reichelt in Kuntze) Hustedt. *Nitzschia sinuata* and *N. heidenii*, however, differ clearly from *N. solgensis* in having a complex type of areolar occlusion (Figs. 13, 15).

Acknowledgements

We wish to thank B. Hartley of Somerset, England, H. Tanaka of Gunma Prefectural Museum of History, and T. Nagumo of the Nippon Dental University for their kind donations of diatom samples for our studies.

Literature Cited

CLEVE, P. T. AND A. GRUNOW. 1880. Beiträge zur Kenntnis der arctischen Diatomeen. K. Svenska Vetenskaps-Akad. Handl. 17:1–121.

CLEVE-EULER, A. 1952. Die Diatomeen von Schweden und Finnland. Teil 5. K. Svenska Vetenskaps-akad. Handl. 3:1–153.

GRUNOW, A. 1862. Die österreichischen Diatomeen nebst Anschluss einiger neuen Arten von andern Lokalitäten. Verh. kais.-königl. zool.-bot. Gesell. Wien 12:315–472, 545–588.

KRAMMER, K. AND H. LANGE-BERTALOT. 1988. Bacillariophyceae. Teil 2. Bacillariaceae, Epithemiaceae, Surirellaceae *in* Süwasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fisher, Jena. 596p.

LANGE-BERTALOT, H. 1980. New species, combinations and synonyms in the genus *Nitzschia*. Bacillaria 3:41–78.

MANN, D. G. 1978. Studies in the family Nitzschiaceae (Bacillariophyta). Ph.D. Dissertation, Univeristy of Bristol.

———. 1981. Sieves and flaps: siliceous minutiae in the pores of raphid diatoms. Pp. 279–300 *in* Proceedings of the 6th Symposium on Recent and Fossil Diatoms, R. Ross, ed. O. Koeltz, Koenigstein.

———. 1984. An ontogenetic approach to diatom systematics. Pp. 113–144 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

VAN HEURCK, H. 1881. Synopsis des Diatomées de Belgique. Atlas, Plates 31–77. Ducaju et Cie, Anvers.

———. 1885. Synopsis des Diatomées de Belgique. Supplement, Plates A–C. Ducaju et Cie, Anvers.

Explanation of Plates

Plate 1, Figures 1–8

FIGURES 1–8. *Nitzschia tabellaria*. FIGURES 1, 2. Whole valves; Figure 1 is a drawing, Figure 2 (LM). Scale bar = 10 µm, sample No. K-1792. FIGURES 3, 4. LM of whole valves. Scale bar = 10 µm, sample No. 2129. FIGURES 5, 6. SEM of oblique views of whole valves, interior and exterior, respectively. Scale bar = 1 µm, sample No. K-2129. FIGURE 7. SEM showing detail of valve areolae. Scale bar = 0.1 µm, sample No. 2129. FIGURE 8. TEM showing valve areolar occlusion with perforations in a hexagonal array. Scale bar = 0.1 µm, sample No. K-2129.

Plate 2, Figures 9–15

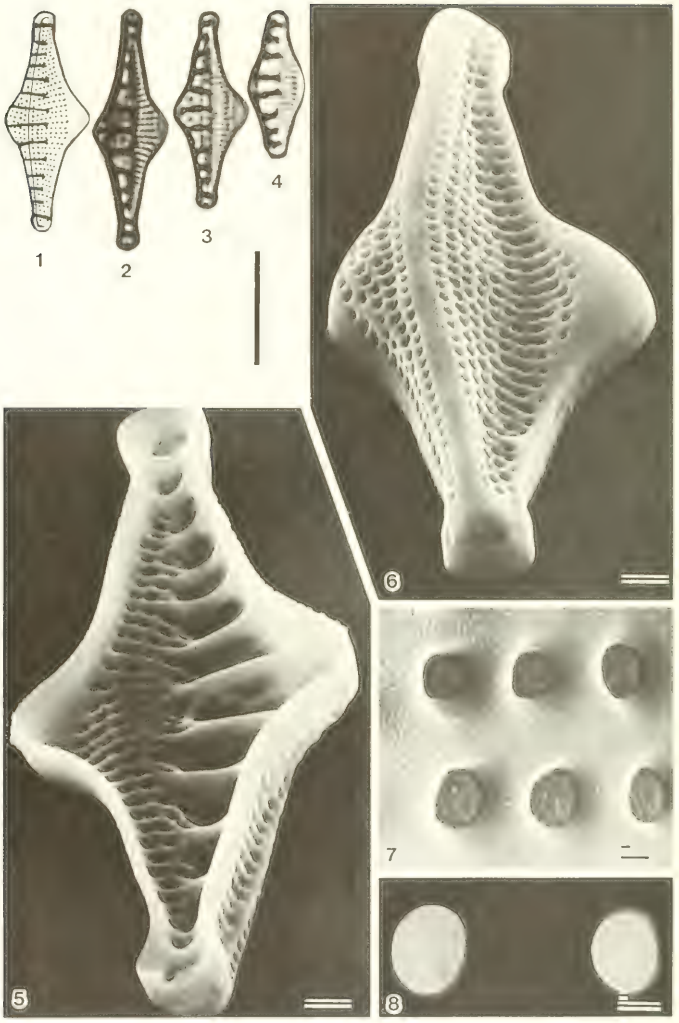
FIGURES 9, 10. *N. tabellaria*, sample No. K-6643. Oblique view (SEM) of whole frustule and schematic representation, respectively, showing epicingulum. Scale bar = 1 µm. FIGURES 11–13. *N. sinuata*, sample No. K-6462. FIGURES. 11, 12. Whole valves (LM). Scale bar = 10 µm. FIGURE 13. SEM view showing detail of valve areolae. Scale bar = 0.1 µm. FIGURES 14, 15. *N. heidenii*, sample No. N-1199. Fig 14. LM view of whole valve. Scale bar = 10 µm. FIGURE 15. SEM view of valve areolae. Scale bar = 0.1 µm.

Plate 3, Figures 16–23

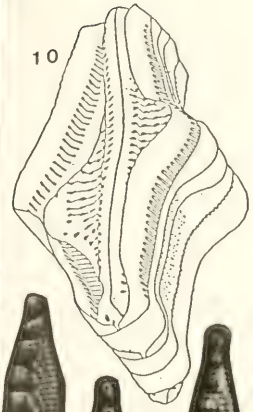
FIGURES 16–23. *N. solgensis*, sample No. K-2153. FIGURES 16–19. Whole valves; Figure 16 is a drawing, Figures 17–19 are LM. Scale bar = 10 µm. FIGURES 20–23. SEM. FIGURES 20, 21. Oblique view of exterior and interior of whole valves, respectively. Scale bars = 1 µm. FIGURE 22. Interior view of whole valve. Scale bar = 1 µm. FIGURE 23. Detail of valve end showing raphe terminal fissure. Scale bar = 1 µm.

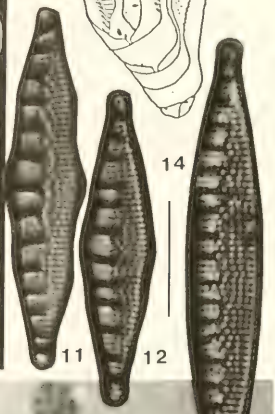
Plate 4, Figures 24–28

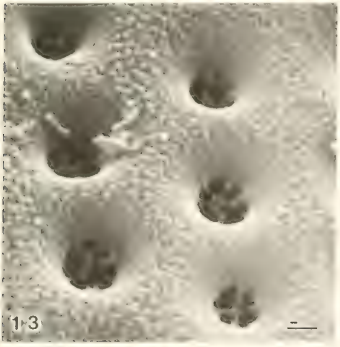
FIGURES 24–28. *N. solgensis*, sample No. 2153. FIGURES 24, 25. Oblique view of whole frustules, showing epicingulum. SEM and illustration, respectively. Scale bars = 1 µm. FIGURE 26. SEM showing detail of frustule terminal with open and closed ends of each band of cingulum. Scale bar = 1 µm. FIGURE 27. TEM view showing areolar occlusions with perforations in a hexagonal array. Scale bar = 0.1 µm. FIGURE 28. SEM view showing detail of external areolar occlusions on the raphe canal (arrows) and on the valve. Scale bar = 0.1 µm.


1
2
3
4
5
6
7
8

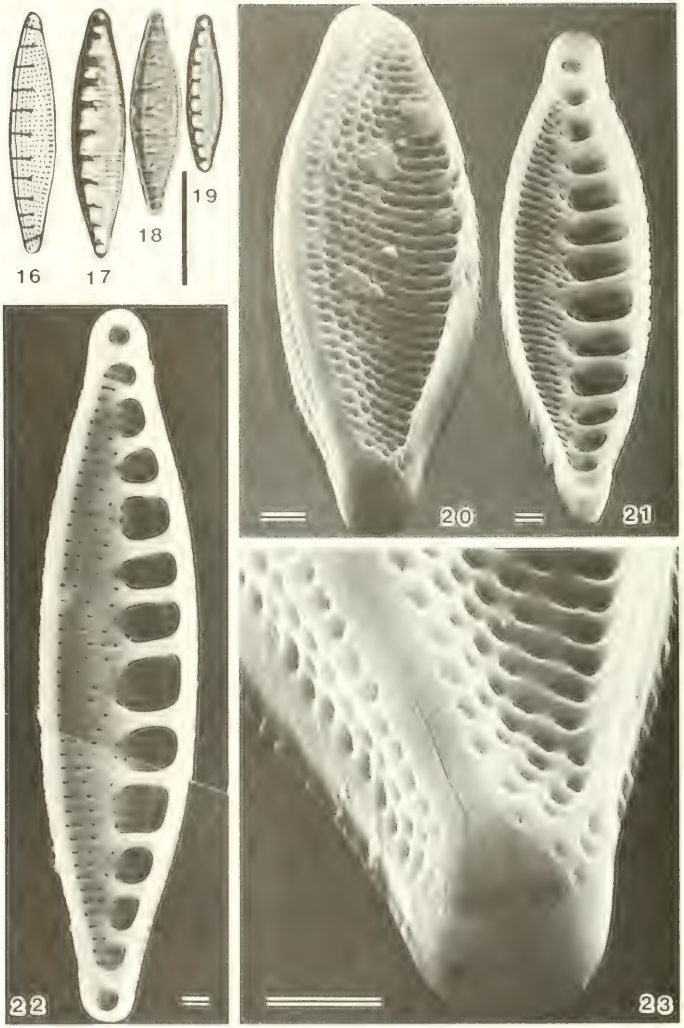
9


10

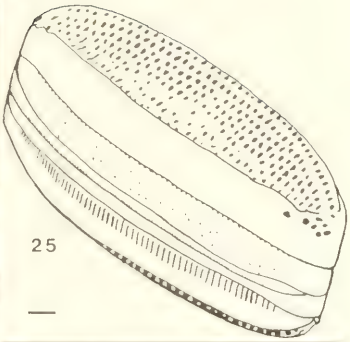

11
12
14

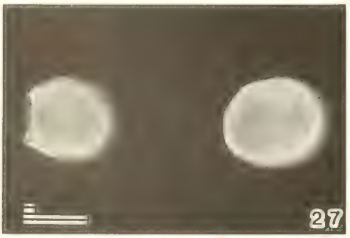

13

15


16
17
18
19
20
21
22
23

24


25


27

26

28

Ultrastructure of *Fragilaria* Lyngbye Species (Bacillariophyta) From Neogene Sediments in Bulgaria

by

N. Ognjanova-Rumenova

Institute of Geology, Bulgarian Academy of Sciences,
"G. Bonchev" 24, 1113 Sofia, Bulgaria

and

D. Temniskova-Topalova and M. Valeva

Biological Faculty, Sofia University,
"D. Zankov" 8, 1000 Sofia, Bulgaria

with 4 plates

Abstract: SEM observations of specimens identified as species of *Fragilaria* from Neogene fossil material allowed us to evaluate the recent generic divisions proposed by Williams and Round (1987) and recently contested by Lange-Bertalot (1989). In all, 294 samples were investigated from marine and non-marine sediments in Bulgaria from the Middle–Late Miocene and Pliocene. Species identified from these samples are: *Fragilaria construens*, *F. construens* var. *venter*, *F. construens* var. *binodis*, *F. construens* var. *subsalina*, *F. istvanffyi*, *F. pinnata*, *F. pinnata* var. *lancettula*, *F. zeilleri*, *F. zeilleri* var. *elliptica*, *F. bituminosa*, *F. transylvanica*, and two unidentified species, *F.* sp. 1 and *F.* sp. 2. The genera *Staurosira*, *Staurosirella*, *Pseudostaurosira*, and *Punctastriata*, described by Williams and Round, and *Opephora* share a number of common features. However, the different areolae structures observed in our specimens were compared to those typical for *Staurosira*, *Staurosirella*, *Pseudostaurosira*, *Punctastriata*, and *Opephora*. A number of transitory forms from one type to another were encountered. In the light of these observations, and the contrasting interpretations of Williams and Round (1987) and Lange-Bertalot (1989), we suggest three alternative solutions to the taxonomy of these species: (1) recognition of the five genera described by Williams and Round (1987); (2) recognition of *Staurosira* at the subgeneric level but to include the genera *Staurosirella*, *Pseudostaurosira*, *Punctastriata*, and *Opephora*; (3) recognition of *Staurosira* at the generic level also to include *Staurosirella*, *Pseudostaurosira*, *Punctastriata*, and *Opephora*.

Introduction

During the last decade the genus *Fragilaria* Lyngbye has attracted the attention of a number of systematists who have produced taxonomic revisions based on the ultrastructure

of different species (Haworth 1975; Lange-Bertalot 1980; Poulin et al. 1986, and others). When differentiating between and among species, alternative ultrastructural features have been used as taxonomic characters by different authors (Marciniak 1982; Williams and Round 1987; Desikachary et al. 1989).

Based on SEM studies of valve and girdle morphology and plastid structure, Williams and Round (1987) described four new genera, *Staurosirella*, *Pseudostaurosira*, *Fragilariforma* (= *Neofragilaria* Williams & Round; see Williams and Round 1988), and *Punctastriata*, and resurrected the old generic name *Staurosira* Ehrenberg. Their results have recently been revised by Lange-Bertalot (1989) to the extent that there are now two different trends in the taxonomic treatment of *Fragilaria* sensu lato encompassing different views on the principles of diatom taxonomy. Each view has a different understanding of the genus category and the value of various ultrastructural features to distinguish genera at the SEM level. There are also different views on the usefulness of features observed in the LM alone: on the one hand, new genera have been established on the basis of features not clearly visible by LM (Williams and Round 1987), whereas, on the other hand, Lange-Bertalot states (1989, p. 104): "Gattungen sollten sich in der Regel auch in LM klar unterscheiden, lassen, evtl. erst nach vorausgegangenem Studium in REM und dann gezielter Suche nach den charakteristischen Kriterien im LM." Further, Lange-Bertalot suggests that these questions should be submitted for discussion at various international panels.

Our SEM observations on *Fragilaria* are based on rich fossil material and have allowed us to evaluate our specimens in the light of the new genera described by Williams and Round (1987). There are a number of features common to *Staurosirella*, *Pseudostaurosira*, *Punctastriata*, *Staurosira*, and *Opephora* such as sternum width, presence or absence of apical pore fields, presence of small mantle plaques, number of rimoportulae, girdle structure, and mantle spines. Differences between genera are most obvious in the type of areolae and the structure of the striae. Our study has focused on the variability of both the areolae and the striae, highlighting some transitory forms we have observed.

Materials and Methods

A total of 294 samples were investigated from Middle–Late Miocene and Pliocene marine and non-marine deposits in Bulgaria. The sediments from northeast Bulgaria, near the town of Balcik (core-drills, S-100, S-103, S-106, S-153a) are marine and date from the Late Miocene (Early–Middle Sarmatian). The sediments from South Bulgaria are non-marine. These include Late Miocene deposits from Sofia basin (v. Katina S-14, v. Goljanovzi S-1, v. Dobroslavzi S-1113, S-1128, v. Ravno pole S-52, v. Dragovischtiza, outcrop); a Miocene deposit from Karlovo basin (S-532); Late Miocene deposits from Goce Delchev basin (v. Garman S-10, S-14, S-23; v. Baldevo S-28, S-31, S-32); and a Pliocene deposit from Samokov basin (v. Kovatchevzi, outcrop).

The SEM work was performed on Jeol 25, Jeol 733, Jeol T300, and Jeol 35 CF microscopes. Terminology principally follows that given in Anonymous (1975) and Ross et al. (1979).

Results and Discussion

Species from the genus *Fragilaria* identified from these deposits are as follows: *Fragilaria construens* (Ehrenberg) Grun., *F. construens* var. *venter* (Ehrenberg) Grun., *F. construens* var. *binodis* (Ehrenberg) Grun., *F. construens* var. *subsalina* Hust., *F. istvanffyi* Pant., *F. pinnata* Ehrenberg, *F. pinnata* var. *lancettula* (Schum.) Hust., *F. zeilleri* Hérib., *F. zeilleri*

var. *elliptica* (Hérib.) Gasse, *F. bituminosa* Pant., *F. transylvanica* Pant., and two unidentified species, *F.* sp. 1 and *F.* sp. 2.

Observations on these species revealed areolae types that have been observed for *Staurosira*, *Staurosirella*, *Pseudostaurosira*, and *Punctastriata* along with a number of transitory forms connecting different types together. Using these as differentiae, the species may be classified in the genera described by Williams and Round (1987) as follows:

(1) *Staurosira* would include *Fragilaria construens*, *F. construens* var. *venter*, *F. construens* var. *binodis*, *F. construens* var. *subsalina*, and *F. istvanffyi*.

(2) *Staurosirella* would include *F. pinnata* and *F. pinnata* var. *lancettula*.

(3) *Pseudostaurosira* would include *F. zeilleri* and *F. zeilleri* var. *elliptica*.

(4) *Punctastriata* would include the two unnamed species, *F.* sp. 1 and *F.* sp. 2.

Apart from these species, which exhibit the typical features of the genera, we have identified a number of specimens which appear to exhibit transitory areolae forms. They are listed and described below:

(1) Transitory form between the areolae type of *Staurosira* and *Pseudostaurosira* in the species identified here as *F. bituminosa* and *F. transylvanica*. *Fragilaria bituminosa* is often found in the same deposit along with *F. brevistriata*. In LM they differ in the coarseness of their striae; *F. bituminosa* has been reported with 6.5–8.5 striae in 10 µm and the valve measures 14.0–85.0 µm in length and 4.5–8.0 µm in width (Pantocsek 1889; Rehakova 1980; Loseva 1982), and *F. brevistriata* has been reported with 13.0–17.0 striae in 10 µm and measures 3.5–42.0 µm in length and 2.0–6.0 µm in width (Hustedt 1931; Cleve-Euler 1953; Loseva 1982). Our specimens of *F. bituminosa* measure 15.9–63.6 µm in length and 4.8–9.5 µm in width with 7.0–9.0 striae in 10 µm (Pl. 1, Figs. 1, 2).

Williams and Round (1987) typified the genus *Pseudostaurosira* with *F. brevistriata* in which the striae consist of a few, large round to ovoid areolae with no more than four per striae at the center of the valve, fewer at the poles. The closing plates are delicate and highly branched. There is a wide range of areolae structure in our specimens of *F. bituminosa*; some have only one large, round areolae and resemble the typical type of *Pseudostaurosira* (Pl. 1, Figs. 3a, b). However, none possess closing plates, which may be a preservational artifact. The areolae in other specimens are elongated and elliptical with single cross-bars (Pl. 1, Fig. 4). Others have well developed cross-bars, resembling the structure associated with *Staurosirella* (Pl. 2, Figs. 1–3).

Along with *F. bituminosa*, the Neogene non-marine sediments contain a few specimens identified as *F. transylvanica*, which can be differentiated from *F. bituminosa* by the frequency of striae, 10–15 in 10 µm, and its larger size, 30.2–79.5 µm in length, 4.8–6.4 µm in width (Pl. 1, Figs. 5a, b). Our specimens agree well with those described by Rehakova (1980). SEM examination of *F. transylvanica* revealed strongly elongated areolae with occasional cross-bars, similar to those observed in *F. bituminosa* (Pl. 1, Figs. 5a, b).

We are thus faced with the question of which genus to place *F. bituminosa* and *F. transylvanica*, when using just the areolae characters.

(2) Transitory form between the areolae type of *Staurosira* and *Staurosirella*, from round through elliptical to linear, often enlarged transversely (Pl. 3, Figs. 1–7).

(3) Transitory form between the areolae type of *Staurosirella* and *Punctastriata*. This transition is observed in the cross-bars of the closing plates (Pl. 4, Figs. 1–4).

(4) The heteropolar forms, tentatively identified here as *Opephora martyi* Hérib. (but see Lange-Bertalot 1990, in press, referred to in Lange-Bertalot 1989) where he notes that heteropolar, "*Opephoroid*"-type forms can be discovered with isopolar species of *Fragilaria* (Pl. 4, Figs. 5–7).

The areolae of these species is of the *Staurosirella* type and, following Lange-Bertalot (1989), may belong to the *F. pinnata* (= *Staurosira pinnata*) group, which includes comparable heteropolar forms, which he differentiated as a subgenus of *Fragilaria*. Our specimens have areolae cross-bars that differ from the marine species of *Opephora* and from *O. olsenii* in particular (Sündback 1987; Lange-Bertalot 1989; Round et al. 1990).

Other transitory forms of areolae structure in Recent diatoms have been illustrated by Lange-Bertalot (1989). For instance, according to Lange-Bertalot (1989), a single species has the areolae type of both *Punctastriata* and *Staurosirella*. Evidence presented here and in Lange-Bertalot (1989) suggest that there are specimens in which the areolae structure is interchangeable between the different types outlined by Williams and Round (1987). However, the genera *Staurosira, Staurosirella, Pseudostaurosira, Punctastriata,* and *Opephora* share a number of common features, such as the absence of rimoportulae, enabling their distinction from *Fragilaria* sensu lato at the rank of either genus or subgenus (Lange-Bertalot 1989). In addition, the evolution of the striae/areolae structure can be traced in the fossil record on the basis of different species of *Fragilaria* observed across a wide stratigraphical range, from the appearance of *Fragilaria* in the Oligocene to the present day.

Our studies, and those of Williams and Round (1987) and Lange-Bertalot (1989) suggest three possibilities: (1) acceptance of the five genera described by Williams and Round (1987); (2) acceptance of *Staurosira*, but at subgeneric level and to include the genera *Staurosirella, Pseudostaurosira, Punctastriata, Opephora,* and the species *F. bituminosa* and *F. transylvanica*; (3) retain the old generic name of *Staurosira* at the generic level also to include *Staurosirella, Pseudostaurosira, Punctastriata, Opephora*, and the species *F. bituminosa* and *F. transylvanica*.

The appropriate decision depends on a generally acceptable understanding of the "genus" category and a common attitude to the taxonomic value of ultrastructural features observed in *Fragilaria* sensu lato. This situation occurs in a number of new genera recently described in the class Centrophyceae (see e.g., Round et al 1990). Problems associated with the category of genus remain controversial.

Finally, we must refer to the problems that non-taxonomists, such as those working in the field of hydrobiology, ecology, stratigraphy, and palaeoecology for instance, are faced with when dealing with constantly fluctuating classificatory systems.

Literature Cited

ANONYMOUS. 1975. Proposals for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53:325–354.

CLEVE-EULER, A. 1953. Die Diatomeen von Schweden und Finnland. K. Svenska Vetenskap-Akad. Handl. fjarde serien 4:1–158.

DESIKACHARY, T., A. PRASAD, AND P. PREMA. 1989. Valve morphology of the marine diatom *Neofragilaria nicobarica* (Bacillariophyceae: Fragilariaceae). Crypt. Algol. 10:305–311.

HAWORTH, E. Y. 1975. A scanning electron microscope study of some different frustule forms of the genus *Fragilaria* found in Scottish Late-Glacial sediments. Br. phycol. J. 10:73–80.

HUSTEDT, F. 1931. Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresegbiete. Pp. 177–320 *in* Kryptogamen-Flora von Deutschlands, Österreichs und der Schweiz. Teil 7, L. Rabenhorst, ed. Akademische Verlagsgesellschaft, Leipzig.

LANGE-BERTALOT, H. 1980. Zur systematischen Bewertung der bandförmigen kolonien bei *Navicula* und *Fragilaria*. Nova Hedwigia 33:723–787.

———. 1989. Konnen *Staurosirella*, *Punctastriata* und weitere Taxa sensu Williams & Round als Gattungen der Fragilariaceae kritischer Prüfung standhalten? Nova Hedwigia 49:79–106.

LOSEVA, E. I. 1982. Atlas pozdmepliotsenvykh Diatomei Prikam'ya. XI Kongressu INQUA, Moskva, Nauk: Leningrad. 204 pp.

MARCINIAK, B. 1982. Late glacial and Holocene new diatoms from a glacial lake Przedni Staw in the Piec Stawow Polskich Valley, Polish Tatra Mountains. Acta Geol. Sci. Hungaricae 25:161–171.

PANTOCSEK, J. 1889. Beiträge zur Kenntnis der fossilen Bacillarien Ungarns. Teil II. Nagy-Tapolcsany, 123 pp.

POULIN, M., L. BERARD-THERRIAULT, AND A. CARDINAL. 1986. *Fragilaria* and *Synedra* (Bacillariophyceae): A morphological and ultrastructural approach. Diatom Res. 1:99–112.

REHAKOVA, Z. 1980. Süsswasserdiatomeenflora des oberen Miozäns in der Tschekoslowakei. Sbornik geologiskychved, paleontologie 23:83–184.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:513–533.

ROUND, F. E., R. C. CRAWFORD, AND D. G. MANN. 1990. The Diatoms. Cambridge University Press. 747 pp.

SUNDBACK, K. 1987. The episammic marine diatom *Opephora olsenii* Möller. Diatom Res. 2:241–249.

WILLIAMS, D. M. AND F. E. ROUND. 1987. Revision of the genus *Fragilaria*. Diatom Res. 2:267–288.

———. 1988. *Fragilariforma*, nom. nov., a new generic name for *Neofragilaria* Williams & Round. Diatom Res. 3:265–267.

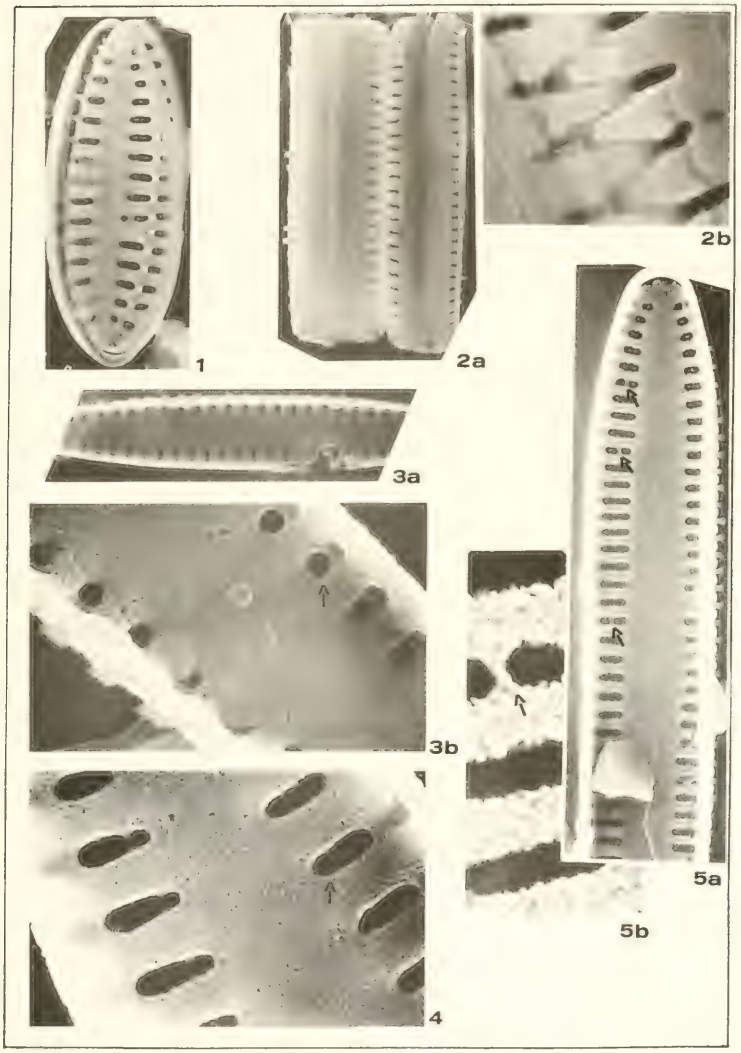
Explanation of Plates

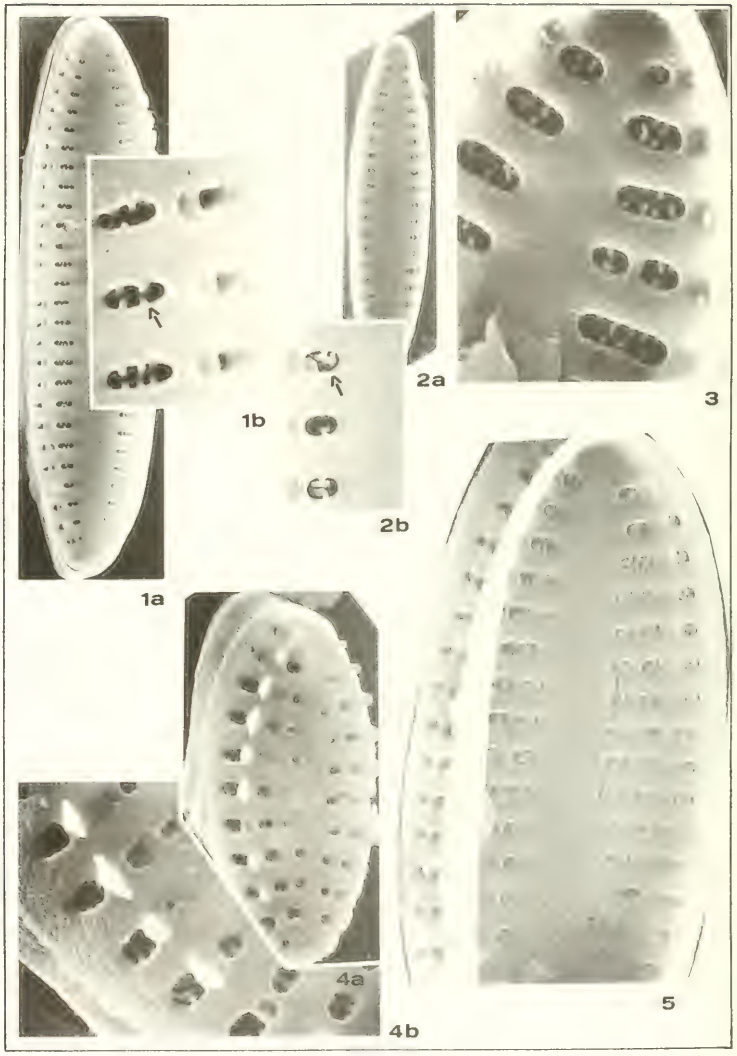
Plate 1, Figures 1–5
FIGURES 1–5. SEM. FIGURES 1–4. *Fragilaria bituminosa* Pant. FIGURE 1. Valve view, × 6000. FIGURE 2a. Mantle view showing linking spines, × 36000. FIGURE 2b. Detail of linking spines, × 18000. FIGURES 3a, b. Valve with large, round areolae, × 5000, × 20000, respectively. FIGURE 4. Valve with elongated, elliptical areolae, × 20000. FIGURE 5. *Fragilaria transylvancia* Pant. FIGURE 5a. Valve view, with single elliptical areolae, fine bars marked with arrows, × 35000. FIGURE 5b. Detail of areolae, × 20000.

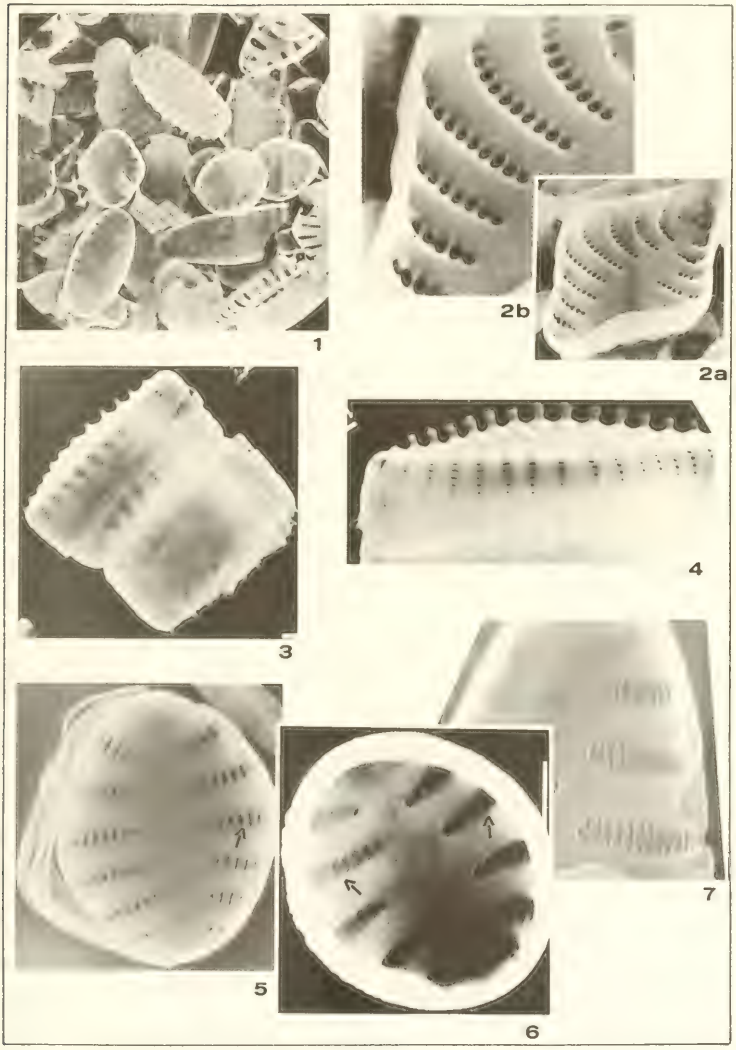
Plate 2, Figures 1–5
FIGURES 1–5. SEM. FIGURES 1–3. SEM. *Fragilaria bituminosa* Pant. FIGURE 1a. Valve view, with areolae intermediate between *Pseudostaurosira/Staurosira*, × 35000. FIGURE 1b. Detail of 1a, × 20000. FIGURE 2a. Valve with branched closing plates, similiar to those observed in *Pseudostaurosira zeillerii*, × 5000. FIGURE 2b. Detail of 2a, × 20000. FIGURE 3. Branched closing plates, × 20000. FIGURE 4. *Fragilaria zeillerii* var. *elliptica*. FIGURE 4a. Whole valve, × 10000. FIGURE 4b. Detail of 4a, × 20000. FIGURE 5. *Fragilaria zeillerii*. × 7500.

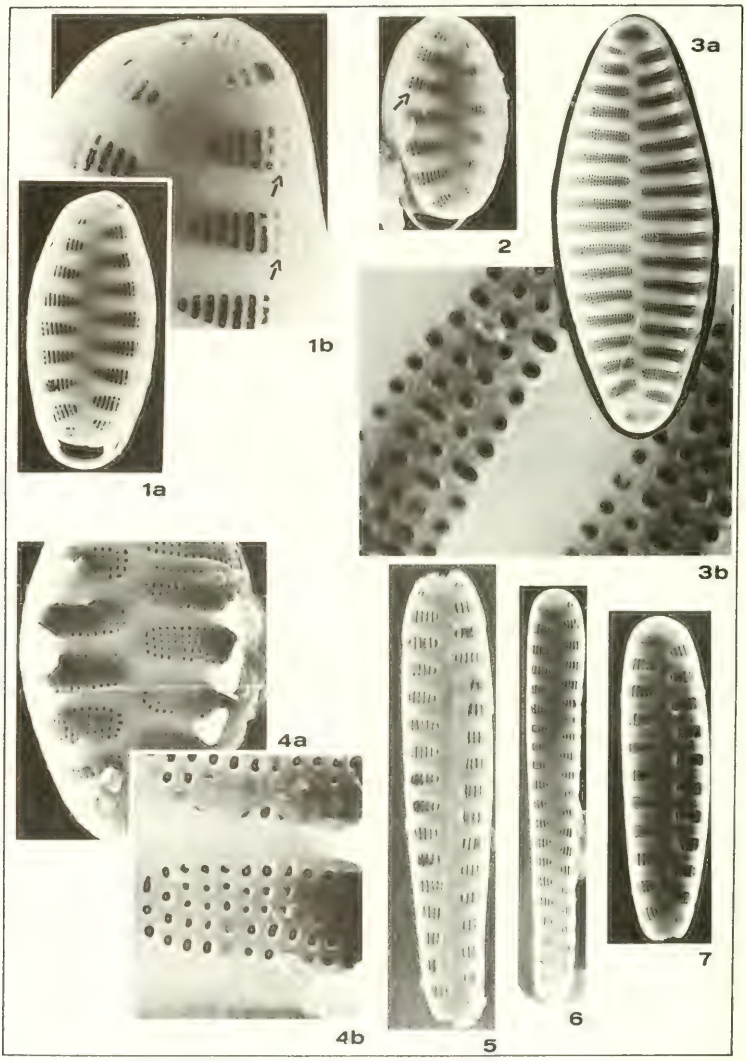
Plate 3, Figures 1–7
FIGURES 1–7. SEM. FIGURES 1–4. *Fragilaria construens*. FIGURE 1. × 4400. FIGURE 2a. Internal view, × 10000. FIGURE 2b. Detail of 2a, × 26000. FIGURE 3. External view, × 12000. FIGURE 4. External view of valve mantle and face, × 8600. FIGURE 5. External view, showing transitory areolae structure between *Staurosira/Staurosirella*, × 12000. FIGURE 6. Internal view showing transitory areolae structure between *Staurosira/Staurosirella*, × 16000. FIGURE 7. Internal view showing type of areolae typical for *Staurosirella*, × 15000.

Plate 4, Figures 1–7
FIGURES 1–7. SEM. FIGURES 1, 2. Transitory areolae structure, between *Staurosira/Punctastriata*. FIGURE 1a. × 6600. FIGURE 1b. Detail of 1a, × 20000. FIGURE 2. × 6000. FIGURE 3. *Fragilaria* sp. 1 (= *Punctastriata* sp.). FIGURE 3a. × 2600. FIGURE 3b. × 26000. FIGURE 4. *Fragilaria* sp. 2 (cf. *Punctastriata ovalis*). FIGURE 4a. × 7500. FIGURE 4b × 2000. FIGURES 5–7. Heteropolar forms, cf. *Opephora martyi*. FIGURE 5. × 7200. FIGURE 6. × 6600. FIGURE 7. × 8600.


1
2a
2b
3a
3b
4
5a
5b


1a
1b
2a
2b
3
4a
4b
5


1
2b
2a
3
4
5
6
7


1a
1b
2
3a
3b
4a
4b
5
6
7

Nonmarine Biostratigraphy of Some Genera of the Class Centyrophyceae From Southern Bulgaria

by

D. Temniskova-Topalova and M. Valeva

Biological Faculty, Sofia University,
"Dr. Zankov" 8, 1000 Sofia, Bulgaria

and

N. Ognjanova-Rumenova

Institute of Geology, Bulgarian Academy of Science,
"G. Bonchev" 24, 1113 Sofia, Bulgaria,

with 2 plates

Abstract: Diatoms from Neogene, nonmarine sediments from Sofia, Samokov, Karlovo, Goe Delchev, and Elchovo basins, southern Bulgaria were examined, and nearly 350 species varieties and forms were identified. The class Centrophyceae is represented by the following genera: *Aulacoseira*, *Melosira*, *Ellerbeckia*, *Actinocyclus*, *Actinocyclus/Coscinodiscus*, *Mesodictyon*, *Concentrodiscus*, *Stephanodiscus*, *Cyclostephanos*, and *Cyclotella*. Both *Actinocyclus* and *Stephanodiscus* developed during the Late Miocene. *Actinocyclus* disappeared gradually during the Late Pliocene while *Stephanodiscus* continued through to the present. *Concentrodiscus* was found to be restricted to Miocene, nonmarine sediments in southern Bulgaria and is therefore considered an index genus for the region. *Aulacoseira*, *Melosira*, *Ellerbeckia*, *Actinocyclus*, *Stephanodiscus*, *Cyclostephanos*, and *Cyclotella* have a wide stratigraphic range and are thus unsuitable as index genera. Some species of these genera, however, have limited stratigraphic distributions (e.g., *Cyclotella iris* var. *integra*, *C. iris* var. *cocconeiformis*).

Introduction

Fossil, nonmarine diatoms of the class Centrophyceae have received a great deal of attention, particularly in the last decade, not only with regard to taxonomy and ultrastructure (e.g., Khursevich 1989), but also systematics (e.g., Theriot and Bradbury 1987) and biostratigraphy (Krebs et al. 1987; Fourtanier and Gasse 1988). This study examines diatoms from Neogene, nonmarine sediments from five basins in southern Bulgaria, and compares their development through time.

Materials and Methods

Diatoms from 16 core-drills and two outcrops of Neogene, nonmarine sediments were studied from Sofia, Samokov, Karlovo, Goe Delchev, and Elchovo basins in southern Bulgaria. Age determinations of the material were based on molluscan and higher plant fossils (Kamenov and Kojumdgieva 1983; Palamarev, pers. comm.). Species abundances were determined by the method of Schrader (1973).

Results

Nearly 350 species, varieties, and forms of diatoms were identified. The class Centrophyceae was represented by the genera *Aulacoseira* Thwaites, *Melosira* Agardh, *Ellerbeckia* Crawford, *Actinocyclus* Ehrenberg, *Mesodictyon* Theriot & Bradbury, *Concentrodiscus* Khursevich, Moisseeva & Suchova, *Stephanodiscus* Ehrenberg, *Cyclostephanos* Round, *Cyclotella* Kütz. *ex* Bréb., and forms that have been referred to both *Actinocyclus* and *Coscinodiscus* Ehrenberg Details of the stratigraphic distributions of species of these genera follow.

Concentrodiscus Khursevich, Moisseeva & Suchova 1989

Concentrodiscus was described originally from Miocene diatomites of Zabaikalie (Khursevich et al. 1989), where it has a stratigraphic range of Middle to Late Miocene. To date, *Concentrodiscus* has been found only in the Late Miocene sediments of southern Bulgaria.

Mesodictyon Theriot & Bradbury 1987

Confirmation of the occurrence of this genus awaits further ultrastructural observations. Our species is very similar to *Mesodictyon* sp. from the Late Miocene of Angola (Fourtanier 1987, Pl. 24, Fig. 11). Rehakova (1980, Pl. 7, Figs. 6, 7) has illustrated *Stephanodiscus* cf. *biharensis* Pant. from the Late Miocene in Czechoslovakia and, in our view, this species may be identical to the *Mesodictyon* specimens found in southern Bulgaria. Our specimens of *Mesodictyon* (?) are known only from the Late Miocene.

Cyclostephanos Round 1982

Cyclostephanos is represented in southern Bulgarian sediments by *C. omarensis* (Kupz.) Khursevich & Loginova and *C. dubius* (Fricke) Round, and these species range from Late Miocene to Early Pliocene. It is interesting to note that *C. omarensis* shows a massive development during the Late Miocene in southern Bulgaria. Khursevich (1989a, pp. 56–57) indicates this species is extinct and typical of the Late Pliocene. Considering the rise and development of *Cyclotella pygmea* Pant. in Oregon (U.S.A.) in the Middle Miocene (Van-Landingham 1985), and the recent transfer of this species to *Cyclostephanos* (Khursevich 1989a, pp. 58–59), the stratigraphic range of *Cyclostephanos* in nonmarine Neogene sediments in the western United States should be extended to include the Middle Miocene.

Cyclotella Kützing ex Brébisson 1838

Cyclotella first occurs in the fossil record between the Middle and Late Miocene, and develops in mass during the Pliocene (Khursevich and Loginova 1980; Krebs et al. 1987; Khursevich 1989b). *Cyclotella iris* Brun & Hérib., *C. iris* var. *integra* Perag. & Hérib., and an unnamed variety of *C. iris* are found in mass during the late Miocene in southern Bulgaria (Pl. 1, Figs. 3, 5, 6). Other varieties of *C. iris* also have been found, including *C. iris* var. *cocconeiformis* Brun & Hérib., *C. iris* var. *charetonii* Serieyssol (Pl. 1, Fig. 4) and single specimens of *C. iris* var. *ovalis* Brun & Hérib. and *C. iris* var. *combiriensis*

Serieyssol. Other *Cyclotella* species that were often found include *C. ovata* Tynni, *C. andacensis* Ehrlich and *C. radiosa* Grun. & Lemm. Although there is no evidence of *Cyclotella* species in the Middle Miocene, its massive development in the basins we investigated suggest an earlier occurrence of the genus in the stratigraphic record.

Cyclotella continues during the Pliocene, but in smaller numbers and strongly reduced species composition. The "*Cyclotella*" flora in northwest Macedonia, Greece (Gersonde and Velitzelos 1978) is similar to the one found in southern Bulgaria. The development and stratigraphic distribution of *Cyclotella* in the Neogene basins of southern Bulgaria differs from that found in the western United States, where *Cyclotella* may appear at the end of the Middle Miocene (?) and reaches its maximum in the Pliocene. Other areas of massive Late Miocene *Cyclotella* development are the French Central Massif (Ehrlich 1966; Serieyssol 1981, 1984) and Spain (Servant-Vildary 1986a). *Cyclotella radiosa* is known from the Middle–Late Miocene of Siberia and the Far East (Jousé 1952; Moisseeva 1967, 1971; Sheshukova-Poretzkaja et al. 1981).

Stephanodiscus Ehrenberg 1845

Stephanodiscus developed massively during the Late Miocene in the southern Bulgarian basins together with *Actinocyclus* and *Cyclotella*. It is represented by a variety of species, some of which are of quantity 5 on Schrader's scale. These include *S. carconensis* Grun., *S. carconensis* var. *pusilla* Grun., *S.* aff. *armenicus* Khursevich & Pirumova, *S. minutula* (Kütz.) Round, *S. niagarae* Ehrenberg and *S.* sp. (Pl. 2, Figs. 2–6). At the Miocene-Pliocene boundary, *S. carconensis* and *S. carconensis* var. *pusilla* develop massively. According to Khursevich (1989b), the oldest deposit of this genus dates from the end of the Early Miocene. *Stephanodiscus* is reported from the Middle Miocene in Austria (Hajos 1970) and from the Late Miocene in Germany (Krasske 1934; Schauderna 1983 cited in Fourtanier 1987). In both China and the western United States *Stephanodiscus* makes its first occurrence in the fossil record at the Miocene-Pliocene boundary and develops in large numbers during the Pliocene (Li and Qi 1986; Krebs et al. 1987).

Melosira Agardh 1824

Only two taxa of the genus *Melosira*, *M. undulata* (Ehrenberg) Kütz. and *M. undulata* var. *normanii* Arnott, were found in our material. *Melosira undulata* var. *normanii* occurred in large numbers in the fixed range 4–5 on Schrader's scale. Both taxa have been observed in Miocene basins in China (Li and Qi 1986), Turkey (Servant-Vildary et al. 1986b), northwest Macedonia, Greece (Gersonde and Velitzelos 1978), Czechoslovakia (Rehakova 1969), Germany (Krasske 1934), and France (Ehrlich 1966).

Ellerbeckia Crawford 1988

Ellerbeckia is represented by two species, *E. kochii* (Pant.) comb. nov. (Basionym: *Melosira kochii* Pantocsek 1892, Beiträge zur Kenntnis der fossilen Bacillarien Ungarns. Teil III. Süsswasser Bacillarien, Pl. 20, Fig. 292) and *E. arenaria* (Ralfs ex Moore) Crawford. The latter species has been reported to extend back to the Oligocene (Abbott and VanLandingham 1972). It is known from Neogene nonmarine sediments in Turkey (Servant-Vildary et al. 1986b), the former U. S. S. R. (Moisseeva 1986), Czechoslovakia (Rehakova 1969, 1980), Austria (Hajos 1970), Germany (Krasske 1934), France (Ehrlich 1966), and Africa (Fourtanier 1987).

Aulacoseira Thwaites 1848

The development of *Aulacoseira* observed in nonmarine basins in southern Bulgaria is the same as that in other Neogene nonmarine basins of the world. The Early and Middle Miocene is marked mainly by the coarsely ornamented forms of *Aulacoseira granulata* (Ehrenberg) Simonsen, *A. granulata* f. "curvata" (Pl. 1, Fig. 1), *A. islandica* (O. Müll.) Simonsen, and *A. islandica* f. "curvata" (described by Jousé 1952 as *Melosira praegranulata* and *M. praeislandica*). Apart from the roughly ornamented species, other forms found in the Late Miocene are similar or identical to modern representatives. The species composition in the Late Miocene includes 20 species, varieties, and forms. *Aulacoseira ambigua* (Grun.) Simonsen and *A. ambigua* f. "curvata" are present in great quantities, and representatives of *A. italica* (Ehrenberg) Simonsen, *A. granulata* var. *muzzanensis* (Meister) Simonsen (Pl. 1, Fig. 2), *A.* cf. *lirata* (Ehrenberg) Ross, and *A. lirata* f. "curvata" are frequent. Although *A. jouseana* (Moiss.) Moiss. is considered a Miocene index species, it is observed in the Neogene sediments of southern Bulgaria in the range of Late Miocene to Early Pliocene.

In general the species composition of *Aulacoseira* does not change during the Late Miocene–early Pliocene, but individual species are found in different quantities. The "curvata" forms, considered to be older, continue their development during the Pliocene with quantities of 4–5 on Schrader's scale.

Actinocyclus Ehrenberg 1837

Included here are species that have in the past been referred to *Actinocyclus* and/or *Coscinodiscus*. Species encountered in our material include *Coscinodiscus miocenicus* Krasske (= *Pontodiscus miocenicus* (Krasske) Moisseeva & Sheshukova-Poretskaya), *C. gorbunovii* Sheshukova-Poretsky (= *Pontodiscus gorbunovii* (Sheshukova-Poretsky) Moisseeva & Sheshukova-Poretskaya), *C. variabilis* Freng., *C. trapeciformis* Rubina, and specimens identified as *Actinocyclus* species (J. P. Bradbury and W. N. Krebs, pers. comm.). Bradbury (1984) has suggested *C. miocenicus* and *C. gorbunovii* may be referred to the genus *Actinocyclus*, due to the presence of a pseudonodule.

The *Actinocyclus* species may be grouped into three types:

(1) Those with short, thick spines that are spread out at their upper part and have a small number (3–4) of rough labiate processes (e.g., *Actinocyclus/Coscinodiscus labatus* Rubina).

(2) Those similar to *Coscinodiscus rothii* (Ehrenberg) Grun. described by Gersonde and Velitzelos (1978, Pl. 1, Fig. 12) from northwest Macedonia, Greece.

(3) *Actinocyclus makarovae* (Temn. & Ognjan.) Temn. & Ognjan., comb. nov. (Basionym: *Pontodiscus makarovae* Temniskova-Topalova & Ognjanova 1990, New species *Pontodiscus* Temnisk. & Ognjanova (Bacillariophyta), Botanischesky Zhurnal, 75:1287, Pls. 1, 2).

The *Actinocyclus* species developed in large numbers and became dominant in the Late Miocene sediments of the Sofia and Karlovo basins. The beginning of the Pliocene is marked by a drop in their quantity and is followed by isolated occurrences of the genus. The massive diffusion of *Actinocyclus* in the Late Miocene in southern Bulgaria is different from the stratigraphic distribution of the genus in the western United States, where *Actinocyclus* developed during the Middle Miocene and disappeared in the beginning of the Late Miocene.

A large variety of *Coscinodiscus* species has been reported from the former U.S.S.R. and are very similar to those found in southern Bulgaria (e.g., *C. miocenicus*, *C. gorbunovii*,

C. lobatus, *C. variabilis*, *C. trapeciformis*, *C. rothii*, *C. rothii* var. *normanii* (Grev.) V.H., Rubina 1967; Moisseeva 1971; Cheremissinova 1973; Khursevich and Loginova 1980; Sheshukova-Poretzkaja et al. 1981).

The "*Coscinodiscus*" species (*C. miocenicus*, *C. variabilis*, *C. stockesianus* (Grev.) Grun. in Pant.) established for the Early and Middle Miocene of Czechoslovakia seem to belong to *Actinocyclus*. The *Actinocyclus* species of Czechoslovakia are also developed mainly in the Early–Middle Miocene (Rehakova 1965).

Discussion

The stratigraphic distribution of members of the class Centrophyceae in nonmarine sediments may be analyzed and compared as follows:

Aulacoseira is found across a wide geographic area throughout the Neogene, with massive development in the Miocene and Early Pliocene. All over the world the Neogene flora of *Aulacoseira* species consists of identical or similar species, including *A. granulata*, *A. islandica*, *A. canadensis* (Hust.) Simonsen., and *A.* cf. *lirata*. The Neogene nonmarine flora is characterized, however, by the genera *Actinocyclus*, *Coscinodiscus*, *Actinocyclus/Coscinodiscus*, *Cyclotella*, *Stephanodiscus*, *Mesodictyon*, and *Concentrodiscus*. Development of *Actinocyclus* and *Stephanodiscus* in the Miocene and Pliocene is not simultaneous between China and western North America (Bradbury 1984; Li & Qi 1986; Krebs et al. 1987). *Actinocyclus* appears at the end of the Early Miocene, develops massively over the Middle Miocene and disappears at the beginning of the Pliocene. *Stephanodiscus*, however, appears at the end of the Late Miocene and reaches its maximum during the Pliocene. In Africa, *Actinocyclus* has not yet been observed, while *Stephanodiscus* has been reported from the Upper Miocene and is present in large numbers during the Pliocene (Fourtanier 1987; Fourtanier and Gasse 1988). In the former U.S.S.R., reports of the earliest occurrence of *Actinocyclus* is from the Late Oligocene, and representatives of this genus are found in the stratigraphic record through to the Early Pliocene (western Siberia, Rubina 1967, 1970; Voszennikova 1969; Pribaical, Cheremissinova 1968, 1971, 1973; Tim River, Siberia, Sheshukova-Poretzkaja et al. 1981; Primor'e, Jousé 1952; Moisseeva 1967, 1971). Khursevich (1989b) indicates *Stephanodiscus* occurs in the stratigraphic record from the end of the Early Miocene to the end of the Pliocene. The two genera develop simultaneously from the Middle Miocene to the Early Pliocene. In the Neogene basins of southern Bulgaria, *Actinocyclus* and *Stephanodiscus* develop simultaneously during the Late Miocene. *Actinocyclus* disappears gradually in the Early Pliocene while at this time *Stephanodiscus* continues to abound. The co-occurrence of *Actinocyclus* and *Stephanodiscus* during this period suggest they are suited to serve as index-genera. A likely candidate to serve as an index genus for southern Bulgaria, however, is *Concentrodiscus*, which is known from this area only in Late Miocene sediments.

The genera *Aulacoseira*, *Melosira*, *Ellerbeckia*, *Actinocyclus*, *Stephanodiscus*, *Cyclostephanos*, and *Cyclotella* all have a wide stratigraphic range, Miocene to recent, and thus cannot serve as index-genera. Some of their representatives, however, have limited stratigraphic distributions and can serve as index-species (e.g., *Cyclotella iris* var. *integra*, *C. iris* var. *cocconeiformis*).

Index-genus and index-species of the classes Centrophyceae and Pennatophyceae (not described here) will help to better identify regional stratigraphy for Neogene nonmarine sediments in Bulgaria.

Literature Cited

ABBOTT, H. AND S. VANLANDINGHAM. 1972. Micropaleontology and paleontology of Miocene nonmarine diatoms from the Harper District, Malheur County, Oregon. Nova Hedwigia 23:846–906.

BRADBURY, J. P. 1984. Fossil *Actinocyclus* species from freshwater Miocene deposits in China and the United States. Pp. 157–171 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

BRADBURY, J. P., K. V. DIETERICH, AND J. L. WILLIAMS. 1985. Diatom flora of the Miocene lake beds near Clarkia in northern Idaho. Late Cenozoic History of the Pacific Northwest. Pac. Div. Am. Assoc. Adv. Sci. Pp. 33–59.

CHEREMISSINOVA, E. 1968. New data on Neogene diatomic flora of Near-Baical region. Pp. 71–74 *in* Fossil Diatoms of the U.S.S.R., A. Jousé, ed. Moscow.

———. 1971. New and interesting diatom species from Neogene sediments, Pribaikaliya. Nov. Syst. Plant. Non-Vasc. 8:52–56.

———. 1973. Diatom flora from Pribaicalie Neogene Deposits. Pp. 1–68, A. Jouse, ed. Novosibirsk.

EHRLICH, A. 1966. Conttribution a l'etude des Gisemens volcano la custers a Diatomées de la region Rochessauve et de Saint Bauzle (Ardeohe). Bull. Soc. Geol. France 8:311–321.

FOURTANIER, E. 1987. Diatomées Neogenes D'Afrique Approche Biostratigraphie en Miliieux Marin (Sud-Ouest Africain) et Continental. These de Doctorat, L'Universite Paris. 291p.

FOURTANIER, E. AND F. GASSE. 1988. Premiers jalons d'une biostratigraphie et evolution des diatomées f'Afrique depuis II. C. R. Acad. Sci. Serie II 306:1401–1408.

GERSONDE, R. AND E. VELITZELOS. 1978. Diatomeenpalaookologie in Neogen-Becken von Vegora N-W Mazedonien (Vorlaufige Mittelung). Ann. Geol. Pars Helleniques 29:373–382.

HAJOS, M. 1970. Kieselgurvorkommen in Tertiarbecken von Aflenz (Steiermark). Mitt. Geol. Gesell. Wien 63:149–159.

JOUSÉ, A. 1952. About history of the diatom flora of the lakes Hanka. Proc. Inst. Geog. Acad. U. S. S. R. 6:226–252.

KAMENOV, B. AND E. KOJUMDJIEVA. 1983. Neogene statigraphy of the Sofia basin. Paleont., Strat. Lithol. Bulgarian Acad. Sci. 18:69–84.

KHURSEVICH, G. 1989a. Atlas of the species of *Stephanodiscus* and *Cyclostephanos* (Bacillariophyta) from the Upper Cenozoic deposits, U.S.S.R., F. Velichkevich (ed.). Minsk. 167p.

———. 1989b. Phylogenetic relationships of some freshwater centric genera of diatoms by reflecting electron micrscopy. Pp. 138–139 *in* Proceedings III Balkan Congress on Electron Microscopy, L. Margaritis, ed. Athens.

KHURSEVICH, G. AND L. LOGINOVA. 1980. The fossil diatom flora of Byelorussia. Garezki, (ed.), 122p. Minsk.

KHURSEVICH, G., A. MOISSEEVA, AND G. SUCHOVA. 1989. New genus of diatoms of the family Stephanodiscaeae. Bot. Zh. 74:1660–1661.

KRASSKE, G. 1934. Die Diatomeenflora der hessichen Kieselgurlager. Sitzungs. Heidelberger Akad. Wissenschaften, 5:1–26.

KREBS, W., J. P. BRADBURY, AND E. THERIOT. 1987. Neogene and Quaternary lacustrine diatom biochronology, western U.S.A. Palaios 2:505–513.

LI, J. AND Y. QI. 1986. Neogene diatom assemblages in China. Pp. 699–711 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard, ed. O. Koeltz, Koenigstein.

MOISSEEVA, A. I. 1967. Continental Neogene diatoms from the South of the Far East and their straigraphic significance. Pp. 267–280 *in* Stratigraphy and Paleontology of Mesozoic and Paleogene-Neogene continental deposits from the Asian part of the U. S. S. R. Leningrad.

———. 1971. Atlas of the Neogene diatoms from the Primorsky region. Z. Gleser (ed.). Leningrad. 152p.

———. 1986. Revision of the freshwater species of genus *Melosira*. Ag. S. L. (Bacillariophyta). Pp. 70–73 *in* Current Questions in Modern Paleontology, B. Sokolov, ed. Kiev.

REHAKOVA, Z. 1965. Fossile Diatomeen der südböhemischen Becker ablagerungen. Rozpravy Ustredniho ustavu geologickeho 32:1–96.

———. 1969. Changements qualitatifs des associations de Diatomees dans le sediments tertiares et quaternaires de Tchecoslovaquie. Pp. 275–285 *in* Etudes sur le Quaternaire dans le Monde, VIIIe, Congres INQUA, Paris.

———. 1980. Süsswasserdiatomeenflora des oberen Miozans in der Tschechoslowakei. Sbornik geoloiskych ved, paleontologie, 23:83–184.

ROUND, F. E. 1982. *Cyclostephanos*—a new genus within the Sceletonemaceae. Arch. Protistenk. 125:323–329.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge. 747 p.

RUBINA, N. V. 1967. Species novae Coscinodisci Ehr. e foramtione Turtassica depresionis Sibiriae Occidentalis. Nov. Syst. Plant. Non-Vasc. 2:63–68.

———. 1970. Diatoms from Cenozoic continental deposits in West Siberian plain and its stratigrpahic significance. Proc. Ind. Inst. Tyumen 1:93–96.

SCHRADER, H.-J. 1973. Proposal for a standardized method of cleaning diatom-bearing deep-sea and land-exposed marine sediments. Nova Hedwigia, Beih. 45:403–409.

SERIEYSSOL, K. K. 1981. *Cyclotella* species of Late Miocene age from St. Bauzil, France. Pp. 27–42 *in* Proceedings of the 6th International Diatom Symposium, R. Ross, ed. O. Koeltz, Koenigstein.

———. 1984. *Cyclotella iris* Brun et Héribaud. Pp. 197–212 *in* Proceedings of the 7th International Diatom Symposium, D. G. Mann, ed. O. Koeltz, Koenigstein.

SERVANT-VILDARY, S. 1986. Fossil *Cyclotella* species from Miocene lacustrine deposit of Spain. Pp. 495–511 *in* Proceedings of the 8th International Diatom Symposium, M. Ricard, ed. O. Koeltz, Koenigstein.

SERVANT-VILDARY, S., J. C. PAICHELER, AND B. SEMELIN. 1986. Miocene lacustrine diatoms from Turkey. Pp. 165–180 *in* Proceedings of the 9th Diatom Symposium, F. E. Round, ed. BioPress Ltd., Bristol and O. Koeltz, Koenigstein.

SHESHUKOVA-PORETZKAJA, V., A. MOISSEEVA, AND O. KOROTKEVICH. 1981. Miocene nonmarine daitom flora from Kompaki Bor region of the Tym River (West Siberia). Pp. 3–101 *in* Diatoms, B. Ipatov, ed. Leningrad.

SIMONSEN, R. 1979. The diatom system: Ideas on phylogeny. Bacillaria 2:9–71.

TEMNISKOVA-TOPALOVA, D. N. AND N. OGNJANOVA–RUMENOVA. 1988. Neogene nonmarine diatoms from sediments of Sofia Valley, Bulgaria. Pp. 91–97 *in* Proceedings of the Nordic Diatomist Meeting, U. Miller & A. M. Robertsson, eds. Stockholm.

———. 1990. A new species of the genus *Pontodiscus* Bot. Zh. 75:1286–1287.

THERIOT, E. AND J. P. BRADBURY. 1987. *Mesodictyon*, a new fossil genus of the centric family Thalassiosiraceae from the Miocene Chalk Hills Formation, western Snake River Plain, Idaho. Micropaleonotlogy 33:356–367.

VANLANDINGHAM, S. L. 1967–1978. Catalogue of the Fossil and Recent Genera and Species of Diatoms and their Synonyms. Vols I–VII. J. Cramer, Lehre.

———. 1985. Potential Neogene Diagnostic diatoms from the western Snake River Basin, Idaho and Oregon. Micropaleontology 31:167–174.

VOZSENNIKOVA, T. F. 1960. Paleoalgological characteristic of Cenozoic deposits from West Siberia plain. Proc. Inst. Geol. Geophys. Acad. Sci. U.S.S.R 1:7–64.

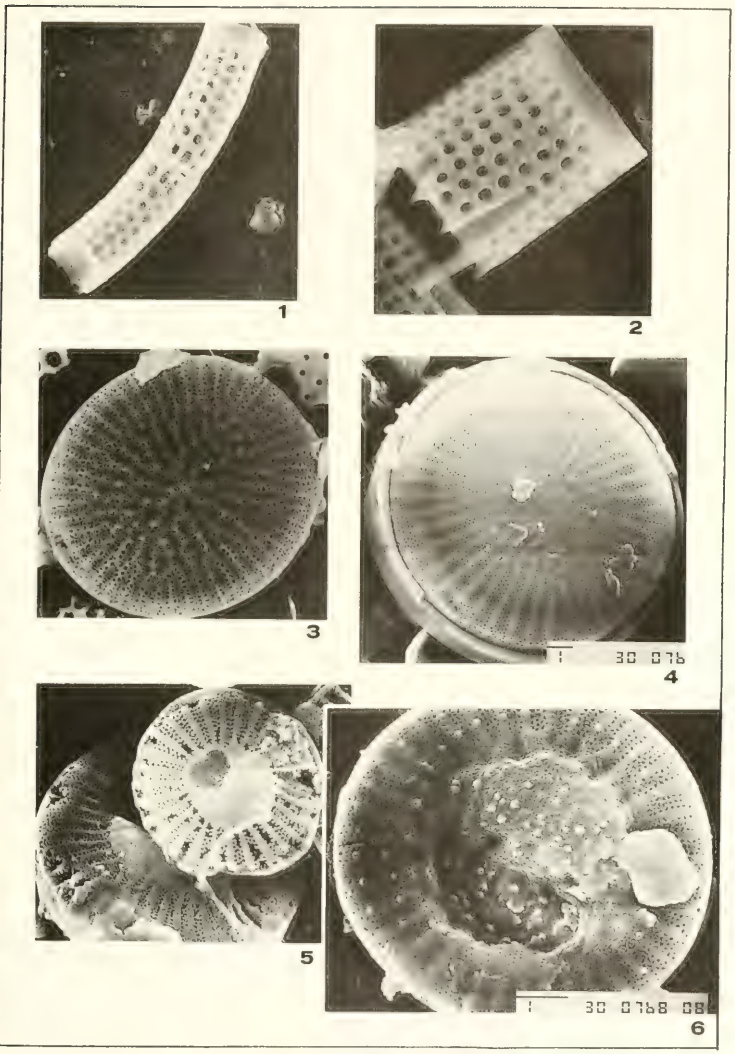
Explanation of Plates

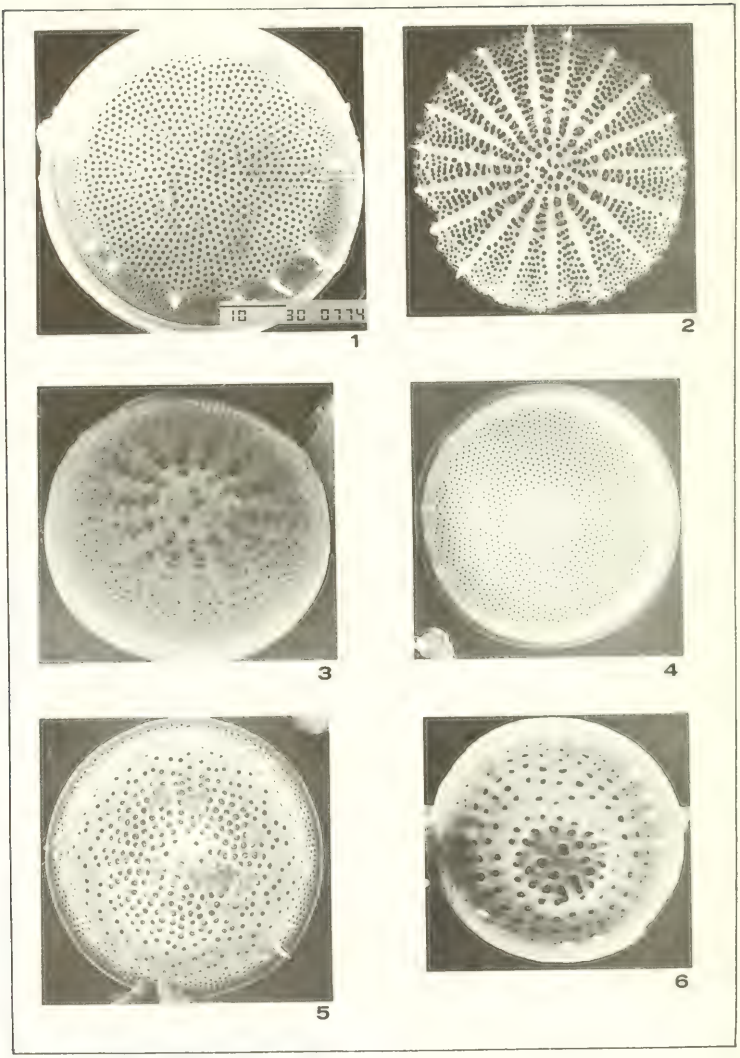
Plate 1, Figures 1–6

FIGURE 1. *Aulacoseira granulata* (Ehrenberg) Sim. f. curvata. × 4400. FIGURE 2. *Aulacoseira granulata* var. *muzzanensis* (Meister) Sim. × 6600. FIGURE 3. *Cyclotella iris* var. *integra* Perag. & Hérib. × 4000. FIGURE 4. *Cyclotella iris* var. *charetoni* (Hérib.) Serieyssol. × 7500. FIGURES 5, 6. *Cyclotella iris*, undescribed variety. × 10,000, × 15,000, respectively.

Plate 2, Figures 1–6

FIGURE 1. *Actinocyclus makarovae* (Temn. & Ognjan.) Temn. & Ognjan. × 2000. FIGURE 2. *Stephanodiscus carconensis* Grun. × 3000. FIGURE 3. *Stephanodiscus* aff. *armenicus* Churs. & Pirum. × 5400. FIGURE 4. *Stephanodiscus* sp. 1. × 3200. FIGURE 5. *Stephanodiscus* sp. 2. × 6600. FIGURE 6. *Stephanodiscus* sp. 3. × 7200.


1
2
3
30 076
4
5
30 0768 08
6


1
2
3
4
5
6

Thalassiosira Species From the Southern Gulf of Mexico

by

Sergio Licea

Instituto de Ciencias del Mar y Limnologia,
Universidad Nacional Autonoma de Mexico, Apartado Postal 70-305,
Mexico 04510 D. F.

with 2 figures, 4 tables, and 6 plates

Abstract: Light, transmission, and scanning electron microscopical observations of field net samples, taken from the Gulf of Mexico between March 1971 and April 1983, revealed the presence of 19 species of *Thalassiosira*. Observations on valve morphology, occurrence, and relative abundance were made for each species. Most specimens agree well with respect to valve morphology as described in the literature. *Thalassiosira delicatula*, *T. diporocyclus*, *T. lineata*, *T. minima*, *T. lineoides*, *T. nanolineata*, *T. partheneia*, and *T. oceanica* were the most abundant species near Cape Catoche during spring, where an upwelling occurs. Typical summer species were *T. elsayedii*, *T. alleni*, *T. oestrupii* var. *venrikae*, *T. punctifera*, *T. sackettii*, and *T. subtilis*. They occurred in waters associated with oligotrophic conditions. Species were arranged in four groups based on valve morphology.

Introduction

Thalassiosira Cleve is one of the largest and most widespread diatom genera, having fossil, marine, and fresh-water representatives. Since Cleve (1873) established this genus, many species have been described. VanLandingham (1978) recorded 73 *Thalassiosira* species, while Fryxell (1978a) mentions that approximately 100 species are recognized. Makarova (1988) indicates that 125 taxa have been described.

Basic valve characteristics of this group include external foramen, internal cribrum, presence of at least one labiate process (rimoportula), and strutted processes (fultoportulae) on the face of the valve (Hasle 1968, 1973b). Presence of occluded processes are considered to have taxonomic value (Fryxell 1975, 1978; Hasle and Fryxell 1977a). Valve size, areolae size, and pattern and placement of the processes as well as nature of the mantle are also considered important taxonomic characters (Fryxell and Hasle 1977). Fryxell et al. (1984) found that location of the labiate processes in relation to the marginal ring of strutted processes is a valuable taxonomic character. Hasle (1983) and Syvertsen and Hasle (1984) found that the number of satellite pores of the strutted processes can be specific for each taxon.

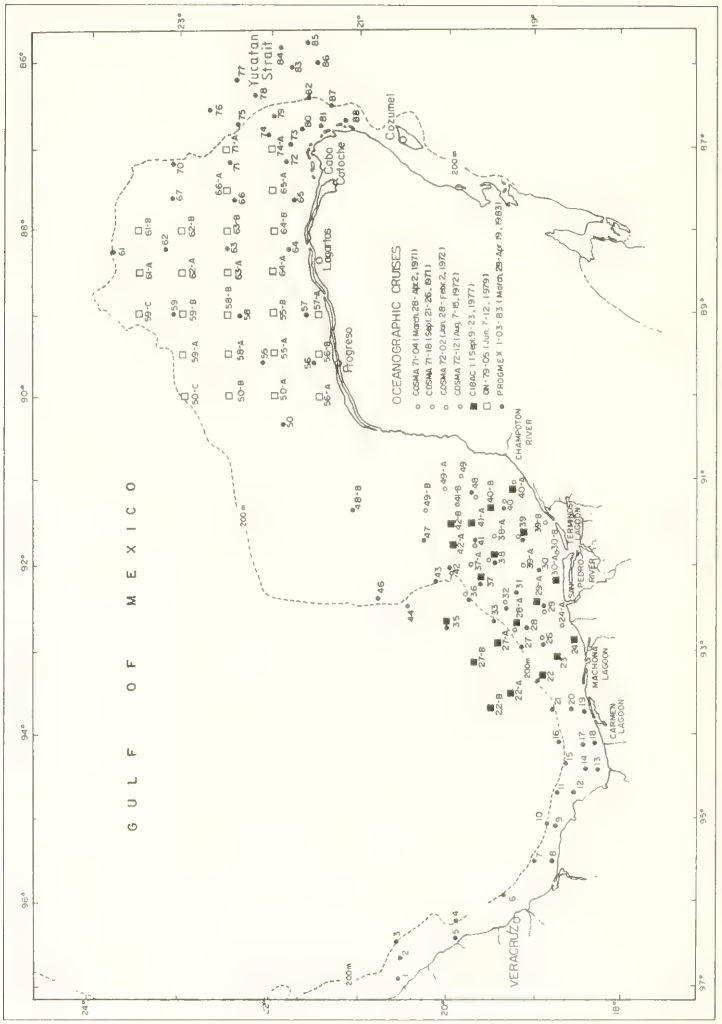


FIGURE 1. Location of study area.

Composition of marine phytoplankton from seven oceanographic cruises of the southern Gulf of Mexico has previously been documented (Licea et al. 1982). This material forms the basis of the *Thalassiosira* species treated in this paper. The valve morphology and distribution of the *Thalassiosira* species encountered are the objectives of the present study.

Materials and Methods

This study is based on vertical net hauls collected at each station with a 35-µm mesh net during seven cruises between March 1971 and April 1983 (Fig. 1).

Samples were acid-cleaned and Hyrax mounts made from the cleaned material (Hasle and Fryxell 1970; Simonsen 1974). Cleaned material was also mounted on stubs or grids for scanning and transmission electron microscopy (SEM, TEM, respectively) observations. Uncleaned specimens were fixed in neutralized formalin and used for water preparations.

SEM and TEM observations were conducted at the Department of Biology, the Electron Microscope Unit for Biological Sciences, University of Oslo, as well as the Institute of Geology, University of Mexico.

Relative abundance data is based on analysis of four permanent slides from each station. Species are referred to as rare (if encountered 1–5 times in the four slides), common (6–20 encounters), or abundant (more than 20 encounters).

Measurements were made using light, TEM, and SEM micrographs. Terminology follows that of Anonymous (1975) and Ross et al. (1979).

Results and Discussion

Taxa examined were arranged in four groups according to their valve morphology. Figure 2 includes some morphologic characters.

GROUP I. *Thalassiosira* species with well-developed strutted processes (Table 1).

Thalassiosira alleni Takano
(Figs. 3–5)

REFERENCES: Takano (1965), p. 4, Fig. 2; Hasle (1978), p. 101, Figs. 100–128; Lange et al. (1983), Figs. 1–6.

Cells solitary or in curved chains, 16–25 µm in diameter. Valves curved with a central concavity. One central strutted process and one marginal row of strutted processes are present. Each strutted process is separated by 5–6 areolae. There is a single marginal labiate process. Areolae on valve face are arranged by sectors 16–18 in 10 µm; areolae on mantle are finer, 42 in 10 µm. The mantle areolae are the most distinctive feature of this taxon.

Thalassiosira alleni is relatively rare, occurring more commonly in early spring and summer in some stations in the central part of the study area. It has been reported from waters off Japan, Hawaii, Gulf of Mexico, Greece, and Africa (Takano 1965; Hasle 1978; Lange et al. 1983). Fryxell et al. (1984) observed *T. alleni* in gelatinous colonies in the Gulf Stream core rings.

Thalassiosira binata Fryxell
(Fig. 6)

TABLE 1 *Thalassiosira* species from South Gulf of Mexico with well-developed strutted processes. Measurements from literature and our observations

Taxon	Author	Diameter (µm)	Areolae in 10 µm face	Areolae in 10 µm margin	Labiate process	Strutted processes valve	Strutted processes margin	Other characters
T. alleria	Takano 1965	8 – 18	22 – 14	40	on margin	one central	one row, separated by 5–6 areolae	areolae in sectors
	This study	16 – 25	16 – 18	42				
T. binata	Hasle & Fryxell 1977	4 – 18	30 – 40	·	on margin, close to a strutted	one central	one row	areolae in radial rows
	Takano 1978	7.5 – 16	–	–				
	This study	4 – 7	A	A				
T. nitida	Takano 1965	4 – 10	25 – 30	50	on margin	one away from center	one row, separated by 3–4 areolae	eccentric linear areolation
	Takano 1976	3.8 – 8.8	–	–				
	This study	5.2 – 7.2	31 – 35	47 – 51				
T. ramsina	Hasle 1980	5 – 14	30 – 40	50	on margin, between two strutteds	two centrals	one row, 3–4 in 10 µm	areolae irregular
	Rivera 1981	6 – 15.5	22 – 35	40 – 50				
	This study	6.8 – 10.4	32 – 38	ca. 50				
T. oceanica	Hasle 1983	3 – 12	–	40 – 60	on margin	one slightly subcentral	one row 3–4 in 10 µm	valve face with radial rows
	Herzig & Fryxell 1987	5 – 19	–	–				
	This study	5.7 – 16.2	A	43 – 58				
T. parthencia	Schrader 1972	8 – 14	-	–	on margin, close to a strutted	one slightly subcentral	one row, 3–4 in 10 µm	linear areolar pattern
	Hasle 1983	9 – 11(?)	40 – 60					
	Fryxell et. al. 1984	4.4 – 12	–	–				
	This study	5.3 – 10.2	45 – 60	A				

A = Absent, – = no data available

REFERENCES: Hasle and Fryxell (1977b), p. 244, Figs. 24–29; Takano (1978), p. 46, Figs. 1–9.

The most relevant features in the light microscope include one row of well-developed marginal strutted processes, one central strutted process, and one marginal labiate process positioned very close to a marginal strutted process.

Rare, only observed along Tuxpan and Lagartos rivers outflow (stations 1–3, 57, and 57A). It has been reported from the inlet of the Mississippi River in the Gulf of Mexico and from Japanese littoral waters (Hasle and Fryxell 1977b; Takano 1978).

Thalassiosira mala Takano
(Fig. 7)

REFERENCES: Takano (1965), p. 1, Pl. 1, Figs. 1–8; Takano (1976), Pls. 1, 2.

Cells single, 5–7 µm in diameter. Valves flat, disc-shaped. There is a single, eccentric strutted process with three satellite pores and a marginal row of strutted processes (each with four satellite pores), each separated by 3–4 areolae. One marginal labiate process is present. Hexagonal areolae on valve face are arranged in a eccentric-linear pattern, 31–35 in 10 µm; finer areolae at margin, 47–51 in 10 µm. Most specimens are heavily silicified.

Rare during spring at stations 40, 49, 66, 71, and rare in winter at stations 39, 40, 49. Takano (1965) described *T. mala* as common in several Japanese bays in gelatinous colonies. Hasle (1976), reported it with a wide distribution from temperate to warm waters.

Thalassiosira minima Gaarder
(Figs. 8–14)

SYNONYM: *Thalassiosira fioridana*

REFERENCES: Gaarder (1951), p. 31, Fig. 18; Hasle (1980), p. 167, Figs. 1–17.

Cells united in chains, 6.8–10.4 µm in diameter. Valves flattened, slightly depressed in the center. The valve possesses two central strutted processes, each with three satellite pores, as well as one marginal row of strutted processes, 3–4 in 10 µm. One marginal labiate process is present. Areolae are irregular in shape and size, being larger in the middle of valve face.

Fairly rare in early spring at some sites surrounding the Yucatan Strait and Cape Catoche, associated with the upwelling area. Rare in late spring in about the same area. It has been referred to as a cosmopolitan species (Hasle 1980). Takano (1981) found *T. minima* in Japanese waters while Herzig and Fryxell (1986) observed it in Gulf Stream warm core rings in the North Atlantic.

Thalassiosira oceanica Hasle
(Figs. 15, 16)

REFERENCE: Hasle (1983), p. 220, Figs. 1–16.

Valves flattened, 5.7–16.2 µm in diameter. Valve face has radial striae while the valve margin is coarsely structured. One marginal labiate process is positioned close to a strutted process. A single row of marginal strutted processes is regularly spaced (3–4 in 10 µm), and each process has four satellite pores. Strutted processes are of the operculate type. One slightly subcentral strutted process is present and has three satellite pores.

This species is fairly abundant during spring, and common in early summer near Cape Catoche. It is associated with the upwelling area (stations: 65-A, 66, 71–74, 78–79). It

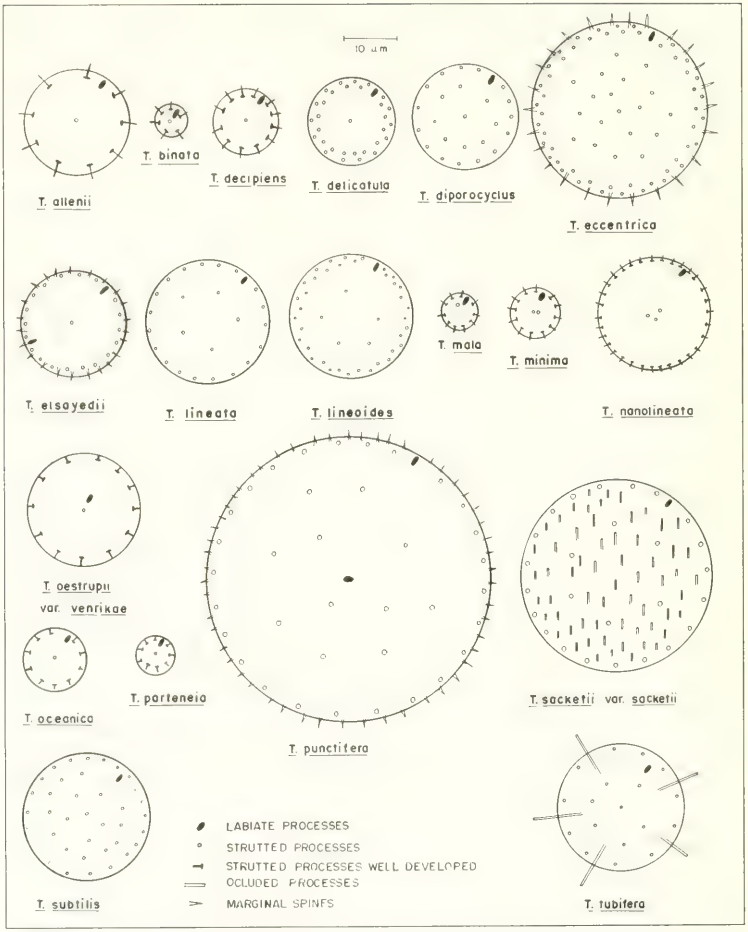


FIGURE 2. Stylized drawings of *Thalassiosira* species. The size of drawings is about the mean valve found.

is reported as an oceanic species in both the Atlantic and Pacific oceans (Hasle 1983; Herzig and Fryxell 1986).

Thalassiosira partheneia Schrader
(Figs. 17–19)

REFERENCES: Schrader (1972), p. 59, Pls. 1, 2; Hasle (1983), p. 223, Figs. 19–31; Fryxell et al. (1984), p. 143, Figs. 2–15.

Cells observed in gelatinous colonies. The valve is fairly flat, disc-shaped, and measures 5.3–10.2 µm in diameter. One marginal labiate process is located between two strutted processes, sometimes closer to one of them. A single row of marginal strutted processes is present, the processes are spaced regularly (3–4 in 10 µm), and each has three satellite pores. Strutted processes are of the operculate type. One subcentral strutted process is present; it has four satellite pores. Basic areolar pattern is radial and fasciculate. Areolae are locular, 45–60 in 10 µm.

This species and *T. oceanica* occurred together and have similar relative abundances in most of the localities examined. Elbrächter and Boje (1978) found it in huge gelatinous colonies in the northwest African upwelling area.

GROUP II. *Thalassiosira* species with eccentric pattern of areolae (see Table 2).

Thalassiosira decipiens (Grunow) Jorgensen
(Figs. 20, 21)

REFERENCES: Hasle (1979), p. 88, Pls. 1–8; McMillan and Johansen (1988), p. 309, Figs. 3–24.

This species occurred as single cells only. The valve face is concave to vaulted, 9–15 µm in diameter. Hexagonal areolae are arranged in an eccentric pattern, 6–8 in 10 µm on valve face; 11–12 in 10 µm on valve mantle. One prominent labiate process is located between two marginal strutted processes. This species has one marginal row of fairly prominent strutted processes, 4–7 in 10 µm, as well as a single strutted processes adjacent to the central areola.

This species was rare, being found only in summer and autumn along the coast, near the outflows of some rivers and coastal lagoons. Hasle (1979) and McMillan and Johansen (1988) report *T. decipiens* from estuarine waters of varying salinities.

Thalassiosira eccentrica (Ehrenberg) Cleve
(Figs. 22–26)

REFERENCES: Fryxell and Hasle (1972), p. 300, Pls. 4, 5; Simonsen (1974), p. 9, Pl. 2, Figs. 1–13; Rivera (1981), p. 64, Pls. 20–22.

Some cells observed united in chains. Valves flat, 17–49 µm in diameter. Areolae of the valve face slightly shorter than those at the margin, 5–8 (12) at the center and 7–10 at the margin. One prominent labiate process at the margin. A single, large central strutted process is present, while other strutted processes are slightly smaller and scattered on the valve face. Both types of strutted processes have four satellite pores. Two rows of alternating marginal strutted processes occur and number 7–8 in 10 µm. Irregular spines are present at margin. Rows of areolae are curved eccentrically.

This species is widely distributed. It is fairly abundant in spring and winter, and common to rare all year around. This species has been characterized as cosmopolitan by Fryxell and Halse (1972), Simonsen (1974), and Rivera (1981).

Thalassiosira elsayedii Fryxell
(Fig. 27)

REFERENCE: Fryxell (1975), p. 59, Figs. 1–13.

TABLE 2 *Thalassiosira* species from South Gulf of Mexico with eccentric pattern. Measurements from literature and our observations.

Taxon	Author	Diameter (µm)	Areolae in 10 µm face	Areolae in 10 µm margin	Labiate process	Strutted processes valve	Strutted processes margin	Other characters
T. decipiens	Hasle 1979	9 - 40	8 - 12	10 - 15	between two marginal strutted	one central	one row, 4 - 7 in 10 µm	labiate and marginal strutted prominents
	This study	9 - 15	6 - 8	11 - 12				
T. eccentrica	Fryxell & Hasle 1972	12 - 101	5 - 8	7 - 9		one central, some scattered	two rows, 7 - 8 in 10 µm	areolae in straight rows at margin
	Rivera 1981	18 - 48.5	5 - 8	7 - 11	at margin			
	Herzig & Fryxell 1986	27 - 47	6 - 8	8 - 9				
	This study	17 - 49	5 - 12	7 - 10				
T. elsayedii	Fryxell 1975	9 - 43	9 - 12	11 - 14		one central	one row, 4 - 5 in 10 µm	marked marginal spines
	Herzig & Fryxell 1986	15 - 30	10 - 11	8 - 9	two near margin			
	This study	15 - 23	10 - 14	12 - 15				
T. oestrupii v. *venrikae*	Fryxell & Hasle 1980	5.5 - 39	6 - 9	7 - 11	eccentric, away from margin	one eccentric	one row, 7 - 9 areolae apart	strutted processes with long internal tubes
	Rivera 1981	13 - 25	7 - 9	8 - 12				
	This study	9 - 33	8 - 10	9 - 12				
T. punctifera	Simonsen 1974	60 - 90	4.5 - 6	6 - 7	one near margin, one subcentric	many scattered	one row, 4 in 10 µm	little spines on margin
	Herzig & Fryxell 1986	18 - 105	6 - 9	8 - 11				
	This study	53 - 82	6 - 8	7 - 9				

Cells single, valve face disc-shaped, 12–23 µm in diameter. Hexagonal areolae organized in an eccentric pattern, slightly irregular in size, 10–14 in 10 µm on valve face; 12–15 in 10 µm on valve mantle. Two marginal labiate processes are present, on nearly opposite sides of the valve from each other. One row of marginal strutted processes is present, processes number 4–5 in 10 µm. There is a single central strutted process.

Rare, registered only in summer at stations 26, 22, 27-A, 36, and 37 in sites away from the coast.

Thalassiosira oestrupii var. **venrikae** Fryxell & Hasle
(Figs. 28–31)

REFERENCES: Fryxell and Hasle (1980), p. 810, Figs 11–19; Rivera (1981), p. 103, Pls. 43, 44.

Only single cells observed. Valve face disc-shaped, slightly concave, 9–33 µm in diameter. Valve face areolae occur in an eccentric pattern, 8–10 in 10 µm, slightly shorter on valve mantle (9–12 in 10 µm). Two processes (a labiate process and a strutted process) on valve face together or slightly separated. One row of marginal strutted processes, the processes separated by 7–9 areolae.

Fairly common in summer, and common in winter near the coast. This species was rare in some stations far from the coast. This variety is widely distributed in tropical and subtropical regions (Fryxell and Hasle 1980; Rivera 1981).

Thalassiosira punctifera (Grunow) Fryxell, Simonsen & Hasle
(Fig. 32)

SYNONYM: *Coscinodiscus excentricus* var. *punctifer*a Grunow

REFERENCE: Simonsen (1974), p. 10, Pls. 2, 3.

Only single cells observed. Valves nearly flat, 53–82 µm in diameter. Valve face areolae occur in an eccentric pattern, slightly irregular in size, 6–8 in 10 µm in the center of the valve, 7–9 in 10 µm near the margin. Two labiate processes are present, one at the margin, the other central. One marginal ring of strutted processes, 4 in 10 µm. Many strutted processes are scattered over the face of the valve. Spines observed on the valve mantle.

Generally rare during summer in some sites away from the coast, common at stations 61, 67, 70, and 59-C in summer.

GROUP III. *Thalassiosira* species with radial fasciculated pattern (Table 3)

Thalassiosira delicatula Ostenfeld
(Figs. 33–36)

SYNONYM: *Thalassiosira coronata* Gaarder

REFERENCES: Hasle (1980), p. 170, Figs. 18–24; Gaarder (1951), p. 30, Fig. 17; Rivera (1981), p. 53, Pls. 10–16.

Cells observed united in chains, 12–21 µm in diameter. Valve face flattened to convex with a concavity in the center. Areolae are irregular in shape and size, 20–23 in 10 µm on valve face, slightly finer on margin (34–38 in 10 µm), with short occluded processes. Hexagonal, pentagonal, or rectangular areolae are arranged in a radial, fasciculated pattern. One labiate process occurs near the margin. A single central strutted process is present

TABLE 3. *Thalassiosira* species from South Gulf of Mexico with radial fasciculated pattern. Measurements from literature and our observations.

Taxon	Author	Diameter (μm)	Areolae in 10 μm face	Areolae in 10 μm margin	Labiate process	Strutted processes valve	Strutted processes margin	Other characters
T. delicatula	Gaarder 1951	9 - 35	—	—	nearly from margin	one central	two alternating rows	areolae variable in size
	Hasle 1980	9 - 30	22 - 26	—				
	Rivera 1981	9 - 25	24 - 33	—				
	Herzig & Fryxell 1986	7 - 10	35 - 38					
	This study	12 - 21	20 - 33	34 - 38				
T. diporocyclus	Hasle 1972	12.5 - 19	20 - 38	—	on valve mantle	one ring midway, one central	one row, 3-4 in 10 μm	areolae usually hexagonal
	Rivera 1981	12 - 18	24 - 31	—				
	Fryxell 1975	12 - 24	26 - 28	—				
	Herzig & Fryxell 1986	15	ca. - 30					
	This study	15 - 24	26 - 28	32 - 36				
T. sacketii	Fryxell & Hasle 1977	43 - 53	(16) 19 - 21	(11) 12 - 14	on margin	one ring, away from margin	one row, 3-4 in 10 μm	areolae tubules present
	Herzig & Fryxell 1986	26 - 62	16					
	This study	36 - 52	18 -23	11 - 14				
T. subtilis	Hasle 1972	17 - 28	30 - 36	—	away from margin	one central and scattered	one row	areolae hexagonal, regular in shape
	Fryxell 1975	18 - 49	30 - 40	—				
	Rivera 1981	16 - 31	30 - 32	—				
	Herzig & Fryxell 1986	20 - 60	ca. - 30					
	This study	18 - 28	32 - 38	32 - 40				
T. tubifera	Fryxell 1975	19 -33	ca. - 20	—	away from margin	one central and irregular ring	one row, 2-3 in 10 μm	presence on occluded processes
	Herzig & Fryxell 1986	(13) 19 - 33	20	—				
	This study	17 - 29	18 - 20	A				

A = Absent, — = no data available, ( ) = extreme values

with 4–5 satellite pores. There are two or three alternating rows of operculated strutted processes, each with 3–4 satellite pores.

Rare to common in some stations near Yucatan Strait and Cape Catoche during early spring. This species has a wide distribution from tropical to temperate waters (Halse 1980; Gaarder 1951; Rivera 1981).

Thalassiosira diporocyclus Hasle
(Figs. 37–40)

REFERENCES: Hasle (1972), p. 113, Figs. 25–45; Rivera (1981), p. 60, Pls. 17–19.

Only single cells seen. Valve almost flat in the center and extremely curved at margin, 15–24 µm in diameter. Areolae are usually hexagonal, and occur in a radial, fasciculated pattern. Areolae on the valve face are larger than those on the mantle, and number 26–28 and 32–36 in 10 µm, respectively. One labiate process occurs on the valve mantle, and its internal expression is larger than its external expression. Strutted process include one row of strutted processes on the margin, one ring located midway on the valve face, and a single central process with four satellite pores.

Common to abundant in spring and summer in most stations surrounding Cape Catoche. Hasle (1972, 1983) found *T. diporocyclus* in great quantities in gelatinous colonies in the upwelling area of Cape Town, and it is also present in the Atlantic Ocean and Gulf of Mexico. Rivera (1981) reported this species from North Chilean waters, while Herzig and Fryxell (1986) observed it in the North Atlantic.

Thalassiosira sacketti Fryxell
(Figs. 41, 42)

REFERENCE: Fryxell and Hasle (1977), p. 75, Pl. 6, Figs. 35–39.

A secondary pattern of spiral rows is present on the valve face. Valve face areolae located towards the margin are larger than those in center, and number 11–14 and 18–23 in 10 µm, respectively. Slender tubules arising from granules between areolae are also a distinctive character of this taxon. One marginal labiate process is present, and there is one marginal row of strutted processes, 3–4 in 10 µm. A second row of strutted processes is present one-third of the way from the margin.

Thalassiosira sacketti is fairly common in summer at stations 61, 67, 70, 76–78. Fryxell and Hasle (1977) refer to it as an oceanic, warm water species. The Gulf of Mexico is the type locality of this taxon, and it is also present in the Pacific Ocean.

Thalassiosira subtilis (Ostenfeld) Gran
(Figs. 43, 44)

REFERENCES: Hasle (1972), p. 112, Figs. 1–20; Rivera (1981), p. 123, Pls. 58–60.

This species occurred as single cells only, 18–28 µm in diameter. Valves are disc-shaped, vaulted. Areolae are hexagonal, regular in shape, arranged in radial sectors, 32–38 in 10 µm. One marginal row of strutted processes, a single central strutted process, and processes scattered over the valve face are present. One large labiate process is positioned away from the margin and oriented radially.

This species is generally rare, found only in summer at stations 70 and 75. According to Hasle (1976) this species is considered to have a wide, oceanic distribution. Rivera (1981) found it near 18°16'S to 42°007'S, while Fryxell et al. (1984) and Herzig and Fryxell (1986) observed it in the Gulf Stream warm core rings along the Atlantic coast of the United States.

Thalassiosira tubifera Fryxell
(Figs. 45, 46)

REFERENCE: Fryxell (1975), p. 69, Pl. 5, Fig. 29, Pl. 6, Figs. 30–34.

Only single cells seen. Valves disc-shaped, 17–29 µm in diameter. Areolae in fasciculated sectors, regular in shape, 18– 20 in 10 µm. One marginal row of strutted processes is present, with processes numbering 2–3 in 10 µm. There is one central strutted process and one irregular row of processes. A single labiate process is positioned outside the irregular ring and it has a long external tube. Occluded processes are present.

Thalassiosira tubifera was rare, found occasionally in winter at stations 26, 39, and 41 during COSMA-72-02 cruise. According to Fryxell (1975), this species has been found in the Gulf of Mexico and Pacific Ocean. Herzig and Fryxell (1986) observed *T. tubifera* in oligotrophic waters of the North Atlantic.

GROUP IV. *Thalassiosira* species with linear pattern of areolae (Table 4).

Thalassiosira lineata Jousé
(Figs. 47–51)

REFERENCES: Hasle and Fryxell (1977a), p. 22, Pls. 5, 6; Rivera (1981), p. 80, Pls. 29, 30.

Only single cells seen. Valves flat, 16–32 µm in diameter. Valve areolae hexagonal in rigorous straight rows, 13–19 in 10 µm. One labiate process is located near margin. There is one row of marginal strutted processes, 6–8 in 10 µm, and each process has three satellite pores. Several strutted processes are scattered on valve face and have two satellite pores. Central strutted processes are lacking. Our specimens have finer areolation than reported in the literature.

Generally rare in summer at stations in front of Terminos Lagoon. This species is also fairly frequent in spring near Yucatan Strait and at stations 2, 4, and 16. Hasle (1976) reported *T. lineata* as a warm water species and Fryxell et al. (1979) found it as a common species in the central Pacific. Rivera (1981) observed *T. lineata* in Chilean coastal waters, while Simonsen (1974) found it, although rare, widely distributed in the Indian Ocean.

Thalassiosira lineoides Herzig & Fryxell
(Fig. 52)

REFERENCE: Herzig and Fryxell (1986), p. 16, Figs. 18–29.

Only single cells seen. Valve disc-shaped, slightly convex, 24–35 µm in diameter. Valve areolae almost in straight rows, 16–18 in 10 µm. Marginal areolae slightly larger, 21–24 in 10 µm. Two marginal rows of alternating strutted processes, 4–5 in 10 µm are present, and several strutted processes are scattered over the valve. Our specimens possess finer areolation than reported in the original description. This species is similar to *Thalassiosira lineata*, but *T. lineata* has only one row of marginal strutted processes and a labiate process that is slightly removed from the margin.

Rare, in spring at four stations near Yucatan Strait. Herzig and Fryxell (1986) found it in slope waters of Gulf Stream warm core rings in the North Atlantic.

Thalassiosira nanolineata (Mann) Fryxell & Hasle
(Figs. 53–56)

REFERENCE: Hasle and Fryxell (1977), p. 32, Figs. 74–80.

TABLE 4 *Thalassiosira* species from South Gulf of Mexico with linear pattern. Measurements from literature and our observations.

Taxon	Author	Diameter (µm)	Areolae in 10 µm face	Areolae in 10 µm margin	Labiate process	Strutted processes valve	Strutted processes margin	Other characters
T. lineata	Hasle & Fryxell 1986	9 - 45	8 - 16	—	near margin	some scattered	one row, 6 - 8 in 10 µm	no central strutted processes
	Herzig & Fryxell 1986	28 - 36	8 - 13	—				
	Rivera 1981	12 - 47	8 - 16	—				
	This study	16 - 32	13 - 19	A				
T. lineoides	Herzig & Fryxell 1986	38.5 - 50	9 - 11	—	on margin	some scattered	two alternating rows, 3 - 5 in 10 µm	areolae almost in straight rows
	This study	24 - 35	16 - 18	21 - 24				
T. nanolineata	Hasle & Fryxell 1977	18 - 27	6 - 8	—	on margin	1 - 5 central	one row, 5 - 7 in 10 µm	strutted externally well developed
	This study	11 - 33	6 - 9	14 - 21				

A = Absent, — = no data available

Only single cells seen. Valve disc-shaped, slightly convex, 11–33 µm in diameter. Valve areolae almost in straight rows, 6–9 in 10 µm. Marginal areolae larger, 14–21 in 10 µm. A single labiate process is positioned near the margin. One marginal row of strutted processes, with well-developed external expressions, number 5–7 in 10 µm, and each strutted process has four satellite pores. One to five strutted processes are observed around the central areola.

Fairly abundant at stations 30-B, 40-B, and 39 during spring. Common in spring and winter at most stations located in the central part of the Bay of Campeche. Hasle and Fryxell (1977) refer it as warm water species restricted to inshore waters.

Conclusions

The 19 *Thalassiosira* species presented here require additional study to delineate more clearly their distributional patterns. It is interesting to observe that the smallest species, such as *T. mala*, *T. binata*, and *T. minima*, were found only occasionally, suggesting their absence may be due to the mesh of the collecting net used. Also, the distinctive morphological characters of these nanoplankters are difficult to distinguish in permanent mounts.

The morphological valve characteristics of the specimens studied here agree well with literature reports. Differences in areolation and size diameter of *T. mala*, *T. eccentrica*, *T. elsayeddi*, *T. oestrupii* var. *venrikae*, *T. punctifera*, *T. lineata*, *T. lineoides*, and *T. nanolineata* (Tables 1–3) were found. However, such characteristics are of low taxonomic value and may be due to phenotypic variance influenced by environmental factors, as has been demonstrated by a number of workers (Hasle et al. 1971; Hasle 1973a; Fryxell and Hasle 1972; Fryxell 1976; Fryxell et al. 1981; Syvertsen 1977; Wood et al. 1987; McMillan and Johansen 1988). Variability of the position of labiate and strutted processes within species was fairly constant in our samples.

Of the species considered in this report, *T. delicatula*, *T. diporocyclus*, *T. lineata*, *T. minima*, *T. lineoides*, *T. nanolineata*, *T. partheneia*, and *T. oceanica* appear to be the best suited as indicators of the surrounding Cape Catoche area, where Ruíz-Renteria and Merino-Ibarra (1989) and Licea et al. (1990) found a zone of high nutrient concentrations during spring and summer. Most of these species occurred at limited sites associated with nutrient-rich waters.

Typical summer species included *T. elsayeddi*, *T. alleni*, *T. oestrupii* var. *venrkae*, *T. punctifera*, *T. sacketii*, and *T. subtilis*. They occurred offshore or in inshore waters with oligotrophic conditions. *Thalassiosira eccentrica* was the only species found throughout the year. It was most the widespread taxon and had little increase in cell numbers during spring. *Thalassiosira decipiens* and *T. binata*, which may occur in fresh and brackish waters, were found after the rainy season near river outflows or close to coastal lagoons. Lowered salinity may have been an important factor for their distribution.

Acknowledgments

I am very thankful to professors G. A. Fryxell (Texas A & M University) and Grethe R. Hasle (University of Oslo) to whom this paper is dedicated. I also thank them for taxonomic advice and their personal hospitality during my stay at their institutions. I am deeply indebted to Austin Ayala-Castanares for academic support and encouragement, and to Ruth Luna and Sergio Licea Jr. for assistance in typing. I also acknowledge the assistance I received from the staff of the Section of Marine Botany and Electron Microscope Unit, Department of Biology, University of Oslo. This investigation was partially supported by

the National Council for Science and Technology.

Literature Cited

ANONYMOUS. 1975. Proposals for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53:323–354.

CLEVE, P. T. 1873. On diatoms from the Arctic Sea. Bih. Konglig Svenska Vetenskaps-Akad. Handl. 1:1–28.

ELBRACHTER, M. AND R. BOJE. 1978. On the ecological significance of *Thalassiosira partheneia* in the Northwest African upweling area. Pp. 24–31 *in* Upweling ecosystems, R. Boje and M. Tomczak, eds. Springer Verlag, New York.

FRYXELL, G. A. 1975. Three new species of *Thalassiosira*, with observations on the occluded process, a newly observed structure of diatom valves. Nova Hedwigia, Beih. 53:57–75.

———. 1976. The position of the labiate process in the diatom genus *Skeletonema*. Br. phycol. J. 11:93–99.

———. 1978a. The genus *Thalassiosira*: *T. licea* sp. nov. and *T. angstii* (Gran) Makarova, species with occluded processes. Bot. Mar. 21:131–141.

———. 1978b. Proposal for the conservation of the diatom *Coscinodiscus argus* Ehrenberg, as the type of the genus. Taxon 27:122–125.

FRYXELL, G. A. AND G. R. HASLE. 1972. *Thalassiosira eccentrica* (Ehrenberg) Cleve, *T. symetrica* sp. nov., and some related centric diatoms. J. Phycol. 8:297–317.

———. 1977. The genus *Thalassiosira*: some species with a modified ring of central strutted processes. Nova Hedwigia, Beih. 54:67–98.

———. 1980. The marine diatom *Thalassiosira oestrupii*: structure, taxonomy and distribution. Am. J. Bot. 67:804–814.

FRYXELL, G. A., S. TAGUCHI, AND S. Z. EL-SAYED. 1979. Vertical distribution of diverse phytoplankton communities in the central Pacific. Pp. 203–209 *in* Marine Geology and Oceanography of the Pacific Manganese Nodule Province, J. L. Bischoff and D. Z. Pipere, eds. Plenum, New York.

FRYXELL. G. A., G. J. DOUCETTE, AND G. F. HUBBARD. 1981. The genus *Thalassiosira*: the bipolar diatom *T. antarctica* Comber. Bot. Mar. 24:321–335.

FRYXELL, G. A., R. W. GOULD, JR., AND T. P. WATKINS. 1984. Gelatinous colonies of the diatom *Thalassiosira* in Gulf Stream core rings including *T. fragilis*, sp. nov. Br. phycol. J. 19:141–156.

GAARDER, K. R. 1951. Bacillariophyceae from the "Michael Sears" North Atlantic Deep-Sea Expedition 1910. Report from the Michael Sears North Atlantic Deep Sea Expedition 2:1–26.

HASLE, G. R. 1968. The valve processes of the centric diatom genus *Thalassiosira*. Nytt Mag. Bot. 15:193–203.

———. 1972. *Thalassiosira subtilis* (Bacillariophyceae) and two allied species. Norw. J. Bot. 19:111–137.

———. 1973a. Morphology and taxonomy of *Skeletonema costatum* (Bacillariophyceae). Norw. J. Bot. 20:109–137.

———. 1973b. Thalassiosiraceae, a new diatom family. Norw. J. Bot. 20:67–69.

———. 1974. Some marine plankton genera of the diatom family Thalassiosiraceae. Nova Hedwigia, Beih. 45:1–49.

———. 1976. The biogeography of some marine planktonic diatoms. Deep Sea Res. 23:319–338.

———. 1978. Some *Thalassiosira* species with one central process (Bacillariophyceae). Norw. J. Bot. 25:77–110.

———. 1979. *Thalassiosira decipiens* (Grun.) Jorg. (Bacillariopyceae), Bacillaria 2:85–108.

———. 1980. Examination of *Thalassiosira* type material: *T. minima* and *T. delicatula* (Bacillariophyceae). Norw. J. Bot. 3:167–173.

———. 1983. The marine planktonic diatoms *Thalassiosira oceanica* sp. nov. and *T. partheneia*. J. Phycol. 19:220–229.

HASLE, G. R. AND G. A. FRYXELL. 1970. Diatoms: cleaning and mounting for light and electron microscopy. Trans. Am. Microsc. Soc. 89:469–474.

———. 1977a. The genus *Thalassiosira*: some species with a linear areola array. Nova Hedwigia, Beih. 54:15–66.

———. 1977b. *Thalassiosira conforta* and *Thalassiosira binata*, two new diatom species. Norw. J. Bot. 24:239–248.

HERZIG, W. N. AND G. A. FRYXELL. 1986. The diatom genus *Thalassiosira* Cleve in Gulf Stream warm core rings: taxonomy, with *T. intrannula* and *T. lineoides*, sp. nov. Bot. Mar. 29:11– 25.

LANGE, C., R. N. NEGRI, AND H. R. BENAVIDES. 1983. Algunas especies del genero *Thalassiosira* (Bacillariophyceae) del mar Argentino. Parte 1. Iheringia. Ser. Bot. Porto Alegre 31:9–30.

LICEA, S., R. LUNA, AND P. TORRES. 1982. Evaluacion de los posibles efectos del derrame del Pozo Ixtoc-I sobre las comunidades del fitoplancton y la produccion primaria en la Sonda de Campeche. Informe final. UNAM, Inst. Ciencias Mar Limnol. (Unpublished). 44 pp.

LICEA, S., P. TORRES, AND R. LUNA. 1993. Distribucion vertical del fitoplancton y nutrientes frente a Cabo Catoche: un ciclo nictemeral en abril de 1983. An. Inst. Cienc. Mar Limnol. 23:(in press)

MAKAROVA, I. V. 1988. Diatomaceous algae of the seas of the U. S. S. R.: the genus *Thalassiosira* Cl. Akad. Nauk. Russia. 117 pp.

MCMILLAN, M. AND J. R. JOHANSEN. 1988. Changes in valve porphology of *Thalassiosira decipiens* (Bacillariophyceae) cultured in media of four different salinities. Br. phycol. J. 23:307– 316.

RIVERA, P. 1981. Beiträge zur Taxonomie und Verbreitung der Gattung *Thalassiosira*, Cleve. Bibl. Phycologica 56:1–220.

ROSS, R., E. J. COX, N. I. KARAYEVA, D. G. MANN, T. B. B. PADDOCK, R. SIMONSEN, AND P. A. SIMS. 1979. An amended terminology for the siliceous components of the diatom cell. Nova Hedwigia, Beih. 64:511–530.

RUIZ-RENTERIA, F. AND M. MERINO-IBARRA. 1989. Upwelling off the North coast of Yucatan Peninsula. Pp. 149–160 *in* Proceedings Workshop Mexico-Australia Marine Science, E. Chavez, ed. Merida, Yuc. and Puerto Morelos, Q. Roo, Mexico.

SCHRADER, H. J. 1972. *Thalassiosira partheneia*, eine neue Gallertlager bildende zentrale Diatomee. Meteor Forschungs. Ergeb., Reihe D, 10:58–64.

SIMONSEN, R. 1974. The diatom plankton of the Indian Ocean expedition of RV "Meteor" 1964–1965. Meteor Forschungs. Ergeb., Reihe D, 19:1–107.

SYVERTSEN, E. E. 1977. *Thalassiosira rotula* and *T. gravida*: ecology and morphology. Nova Hedwigia, Beih. 54:99–112.

SYVERTSEN, E. E. AND G. R. HASLE. 1984. *Thalassiosira bulbosa* Syvertsen, sp. nov., an Artic marine diatom. Polar Biol. 3:167–172.

TAKANO, H. 1965. New and rare diatoms from Japanese marine waters I. Bull. Tokai Reg. Fish. Res. Lab. 42:1–10.

———. 1976. Scanning electron microscopy of diatoms IV. *Thalassiosira mala* Takano. Bull. Tokai Reg. Fish. Res. Lab. 87:57–65.

———. 1978. Scanning electron microscopy of diatoms IV. *Thalassiosira binata* Fryxell. Bull. Tokai Reg. Fish. Res. Lab. 94:45–49.

VANLANDINGHAM, S. L. 1978. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Part VII. *Rhoicosphenia* through *Zygoceros*, pp. 3606–4242. J. Cramer, Vaduz.

WOOD, A. M., R. LANDE, AND G. A. FRYXELL. 1987. Quantitative genetic analysis of morphological variation in Antarctic diatoms grown at two light intensities. J. Phycol. 23:42–54.

Explanation of Plates

The following abbreviations apply to Figures 3–65: S = Station; BF = Bright field; PhC = Phase contrast; SEM = Scanning Electron Microscope; TEM = Transmission Electron Microscope. Arrows indicate labiate processes; triangles indicate strutted processes. Site of collection is given for each figure. Scale bars = 10 μm unless otherwise indicated.

Plate 1, Figures 3–14

FIGURES 3–5. *Thalassiosira alleni*. FIGURE 3. SEM. S-79/ON-79-05, frustule in valve view; note labiate process. FIGURES 4, 4a. BF. S-64/ON-79-05, same specimen showing labiate and strutted processes. FIGURE 5. PhC. Valve view. FIGURE 6. *Thalassiosira binata*, PhC, S-64-B/ON-79-05, valve view; labiate process at 1 o'clock. FIGURES 7, 7a. *Thalassiosira mala*. TEM. S-48/COSMA 72-12, valve view showing eccentric strutted process, marginal row of strutted processes and single labiate process. FIGURES 8–14. *Thalassiosira minima*. FIGURE 8. SEM. S-79/ON-79-05, external

valve view; note one marginal labiate and two central strutted processes. FIGURE 9. SEM. S-70/ON-79-05, internal valve view as in Figure 8. FIGURE 10. PhC. S-70/PROGMEX, cells in girdle view. FIGURE 11. TEM. S-39-A/COSMA 71-18, valve view; note two central strutted processes, irregular areolae and one marginal labiate. FIGURE 11a. Detail of two central strutted processes. FIGURE 12. TEM. S-64/ON-79-05, detail of one marginal strutted process. FIGURE 13. TEM. S-64-A/ON-79-05, detail of marginal area; note one labiate and two strutted processes. FIGURE 14. BF. S-63-B/ON-79-05, other specimen; labiate process at 11 o'clock. Scale bars = 1 μm in Figures 6, 7–9, and 11–13.

Plate 2, Figures 15–22

FIGURES 15, 16. *Thalassiosira oceanica*. FIGURE 15. TEM. S-76/ON-79-05, valve view showing radial striation, labiate process, and strutted processes. FIGURE 15a. TEM. Detail of marginal strutted process with four satellite pores. FIGURE 15b. TEM. Detail of central strutted process with three satellite pores. FIGURE 16. TEM. S-76/ON-79-05, detail of valve margin; note one labiate and one strutted process. FIGURES 17–19. *Thalassiosira partheneia*. FIGURE 17. TEM. S-76/ON-79-05, valve view; note radial striation, marginal row of strutted, and one labiate process. FIGURE 18. TEM. S-77/ON-79-05, detail of the subcentral strutted process with four satellite pores. FIGURE 19. PhC. S-77/ON-79- 05, valve view; note labiate process at 2 o'clock. FIGURES 20, 21. *Thalassiosira decipiens*. FIGURE 20. SEM. S-48/COSMA 71-18, external valve view; note one prominent labiate and marginal strutted processes. FIGURES 21, 21a. PhC. S-1/PROGMEX, same specimen at different levels of focus; note labiate and strutted processes. FIGURES 22, 23. *Thalassiosira eccentrica*. FIGURE 22. PhC. S-72/ON-79-05, detail of central area showing strutted processes. FIGURE 23. TEM. S-72/ON-79-05, detail of central area showing strutted processes. Scale bars = 1 μm in all figures except Figures 19, 21, and 22.

Plate 3, Figures 24–32

FIGURE 24–26. *Thalassiosira eccentrica*. Fig 24. SEM. S-55-A/ON-79-05, external valve view; note one marginal labiate process. Rhombics point out marginal spines. FIGURE 25. SEM. S-61-B/ON-79-05, internal valve view as in Figure 24; note scattered strutted processes on valve surface. FIGURE 26. SEM. S- 44/PROGMEX, detail of valve margin showing labiate and strutted processes. FIGURE 27. *Thalassiosira elsayedii*. TEM. S-76/ON-79- 05, valve view; note two labiates, one central strutted processes and eccentric areolation. FIGURES 28–31. *Thalassiosira oestrupii* var. *venrikae*. FIGURE 28. SEM. S-38/COSMA 72-02, internal valve view showing one labiate and one strutted processes together. FIGURE 29. PhC. S-63/ON-79-05, valve view showing eccentric areolation; labiate processes at 1 o'clock. FIGURE 30. SEM. S-27-A/CIBAC-I, detail of internal valve view showing labiate and strutted processes. FIGURE 31. SEM. S-67/PROGMEX, external valve view; note irregularly sized areolae and labiate and strutted processes. FIGURES 32–32b. SEM. S-76/ON-79-05, *Thalassiosira punctifera*, internal valve view showing two labiate processes, one central and one marginal, tilt 60$. Scale bars = 1 μm in Figures 26–28, 30, 31 and 32a, b.

Plate 4, Figures 33–42

FIGURES 33–36. *Thalassiosira delicatula*. FIGURE 33. PhC. S-62-A/ON-79-05, cells in chains in girdle view. FIGURE 34. SEM. S-63-A/ON-79-05, internal valve view; note two alternating rows of strutted processes, and one marginal labiate process. FIGURE 35. TEM. S-58/ON-79-05, detail of central strutted process with five satellite pores. FIGURE 36. TEM. detail of external projections of marginal occluded processes. FIGURES 37–40. *Thalassiosira diporocyclus*. FIGURE 37. SEM. S-76/ON-79-05, external valve view; note radial fasciculated pattern, marginal labiate and strutted processes.

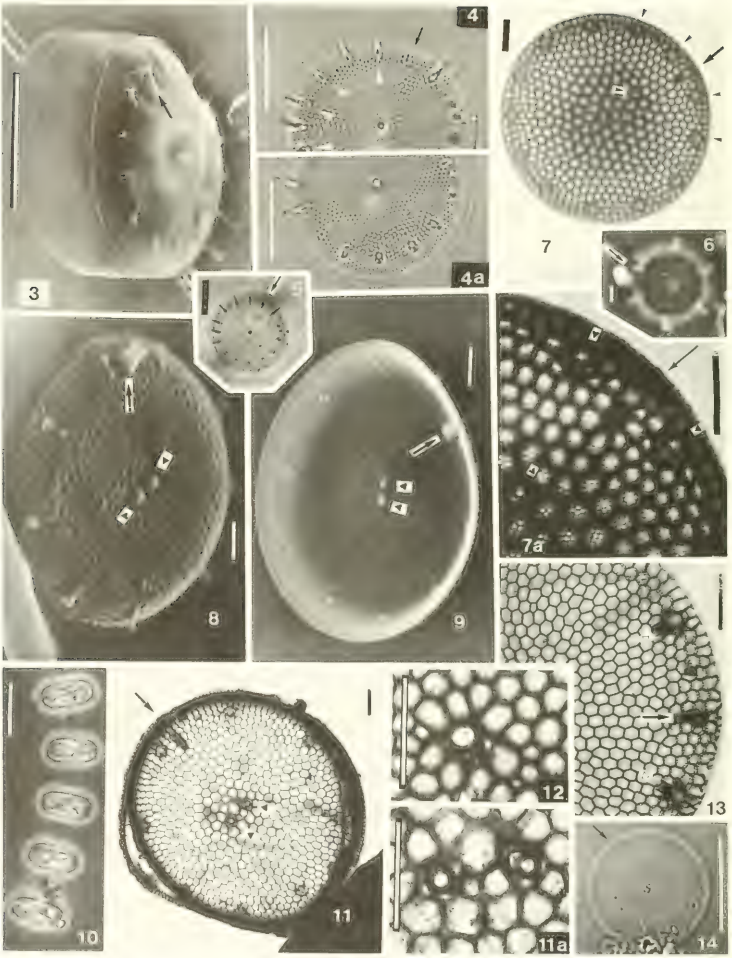
FIGURE 37a. Detail of valve margin showing one labiate and one strutted process. FIGURE 38. TEM. S-76/ON-79-05, detail of central strutted process with four satellite pores. FIGURE 39. SEM. S-71-A/PROGMEX, internal valve view as in Figure 37. FIGURE 40. SEM. S-65/PROGMEX, detail of marginal internal view. FIGURES 41, 42. *Thalassiosira sacketti*. FIGURE 41. SEM. S-76/ON-79-05, frustule in valve view; note labiate process, row of marginal strutted processes and tubules on valve surface. FIGURE 42. SEM. Detail of valve margin showing labiate process and tubules. Scale bars = 1 μm in Figures 35, 36, 37a, 38, 40, and 41.

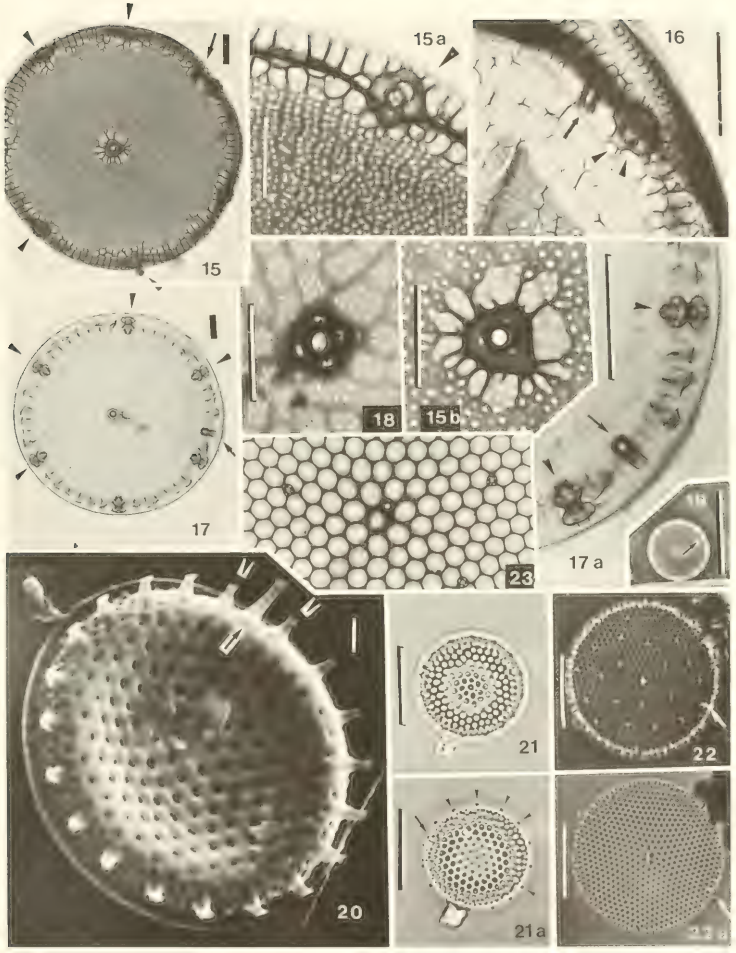
Plate 5, Figures 43–49

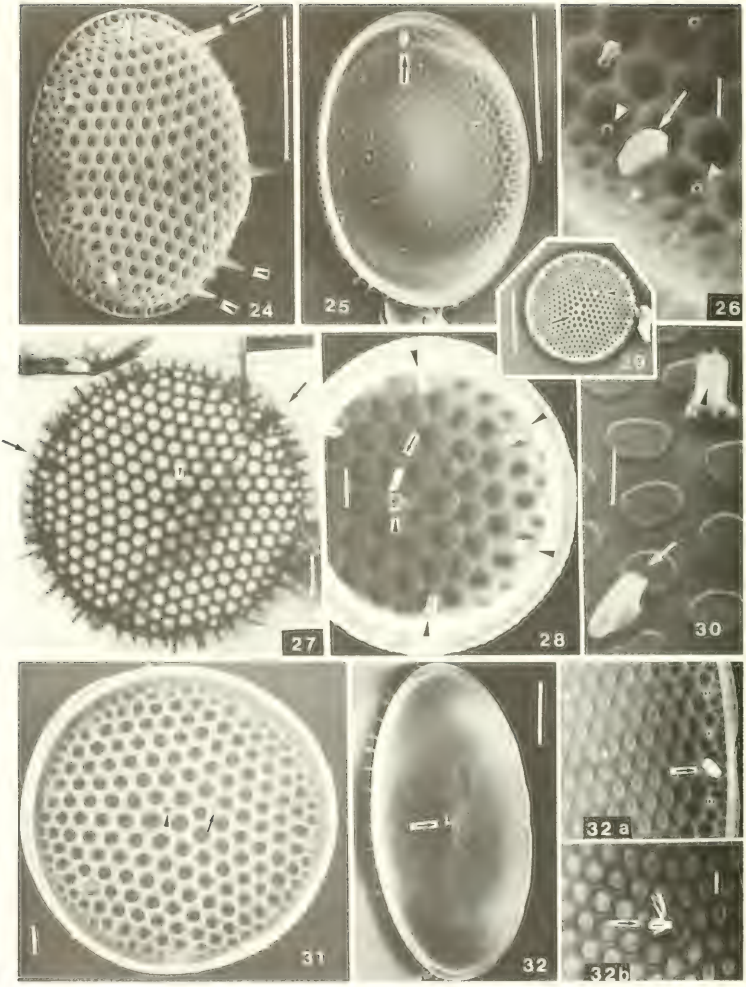
FIGURES 43, 44. *Thalassiosira subtilis*. FIGURE 43. SEM. S-76/ON-79-05, external valve view; note one labiate near margin and one marginal row of strutted processes. FIGURE 43a. Detail of marginal area showing labiate and some strutted processes. FIGURE 44. S-63-B/PROGMEX, detail of internal valve margin as in Figure 43a. FIGURES 45–46a. *Thalassiosira tubifera*. FIGURE 45. SEM. S-63-B/ON-79-05, internal valve view; note labiate process. Triangles point out two occlude processes. FIGURE 46. TEM. S-66-A/ON- 79-05, external valve view showing strutted and occluded processes. FIGURE 46a. Detail of valve margin showing one occluded process. FIGURES 47–49. *Thalassiosira lineata*. FIGURE 47. SEM. Internal valve view showing one labiate process, several strutted scattered on the valve face and one row of marginal strutted processes. FIGURE 48. PhC. S-79/ON-79-05, valve view with focus on margin. FIGURE 49. SEM. S-39/CIBAC-I, detail of valve margin showing labiate and strutted processes. Scale bars = 1 μm in Figures 43a, 44, 46a, 47, and 49.

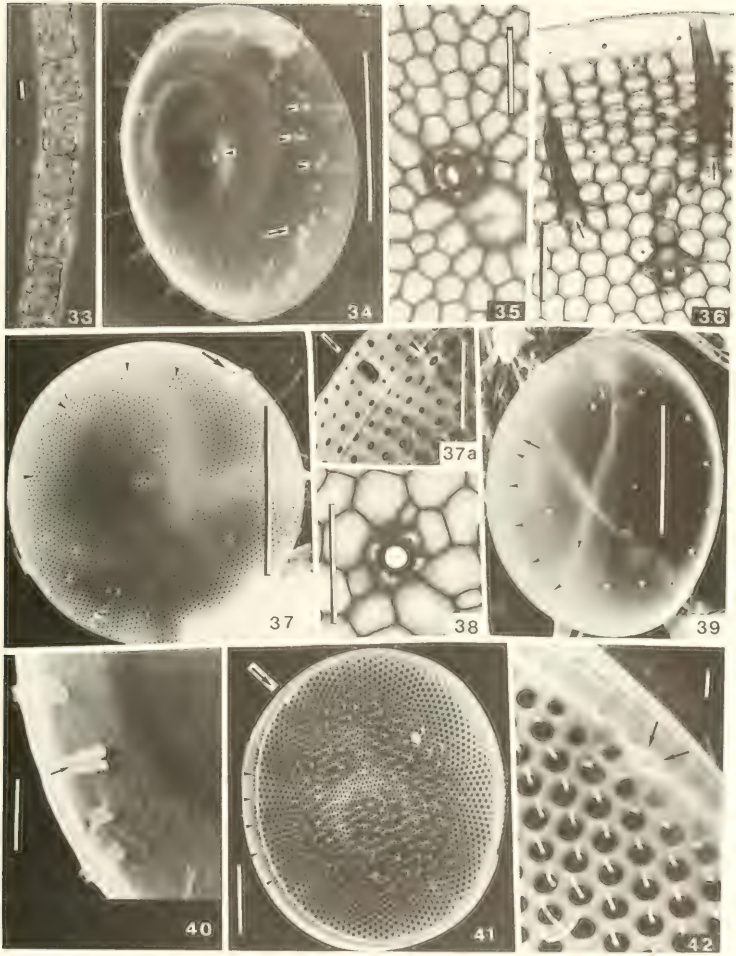
Plate 6, Figures 50–56

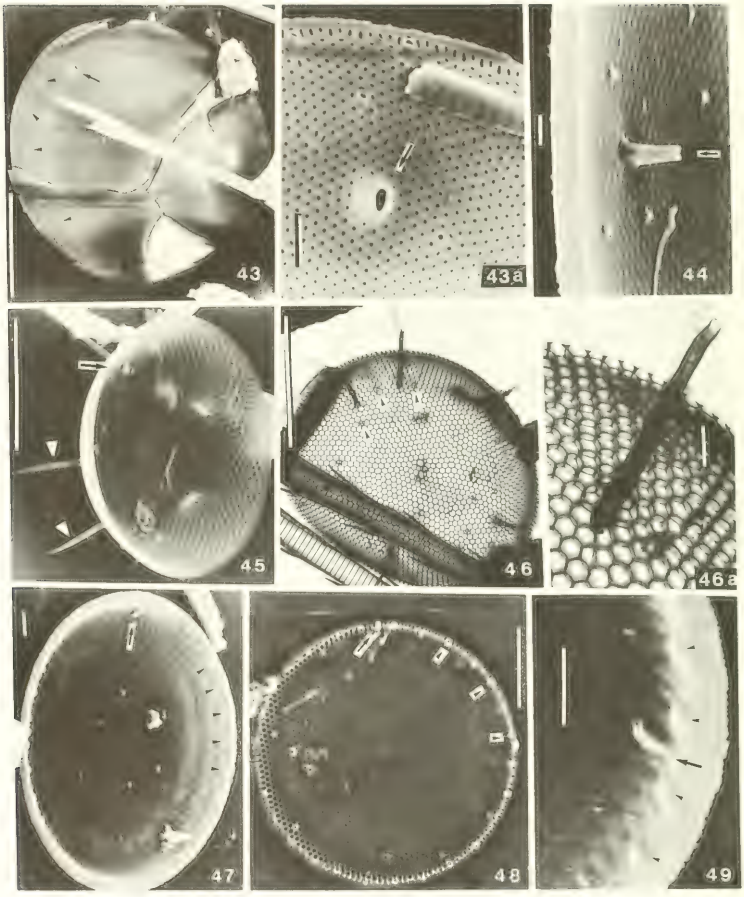
FIGURES 50, 51. *Thalassiosira lineata*. FIGURE 50. TEM. S-79/PROGMEX, detail of central area showing some scattered strutted processes with two satellite pores. FIGURE 51. SEM. S-64-A/ON-79-05, exterior of frustule in valve view. FIGURES 52, 52a. *Thalassiosira lineoides*. FIGURE 52. SEM. S-76/ON-79-05, external valve view; note valve convexity and one labiate process. FIGURE 52a. Detail of valve margin showing one labiate and strutted processes. FIGURES 53–56. *Thalassiosira nanolineata*. FIGURE 53. SEM. S-39-B/COSMA 71-04, external valve view; note labiate process and one row of well developed strutted processes. FIGURE 54. SEM. S-32/COSMA 71-04, detail of valve margin showing labiate and several strutted processes. FIGURE 55. SEM. S-30-B/COSMA 71-04, internal valve view as in Figure 53; note two central strutted processes and one labiate process. FIGURE 56. BF. S-30/PROGMEX, focus on central area; note two central strutted processes. FIGURE 56a. PhC. Same specimen as illustrated in Figure 56, focus on margin showing labiate process. Scale bars = 1 μm in Figures 50, 52a, and 54.

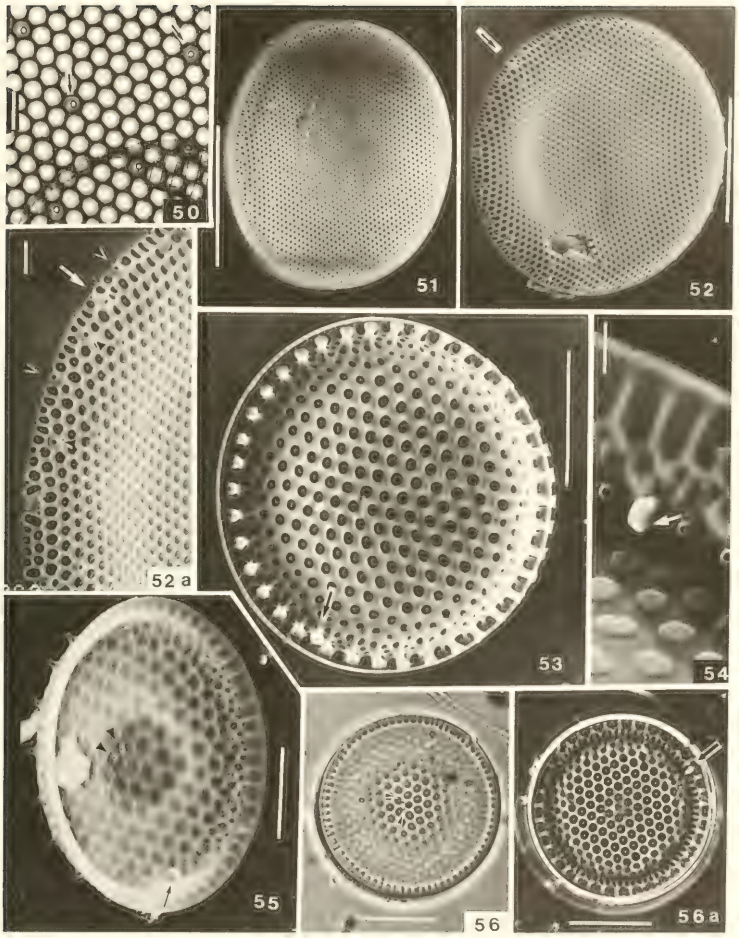

3
4
4a
5
6
7
7a
8
9
10
11
11a
12
13
14


15
15a
16
17
18
15b
17a
23
20
21
22
21a


24
25
26
29
27
28
30
31
32
32 a
32b


33
34
35
36
37
37a
38
39
40
41
42


43
43a
44
45
46
46a
47
48
49


50
51
52
52 a
53
54
55
56
56a

Morphological Variations in Fossil Diatoms from Mono Lake

by

James D. Solliday

Educational Photo Lab, 1130 Austin Street, Santa Ana, California 92704

with 2 figures, 1 table, and 4 plates

Abstract: A diatomaceous deposit from Paoha Island (Mono Lake) has been investigated and the morphology of the four most dominant species described and illustrated. *Anomoeoneis costata* (Kützing) Hustedt, *Surirella utahensis* (Grunow) Hanna & Grant, *Cyclotella bodanica* Grunow, and *S. testudo* Ehrenberg have been identified from the Paoha Island deposit. Abnormalities in the morphology of the *Surirella* species have introduced problems both in terms of taxonomy and information about autecology. None of the species in the fossil material are alive in the lake presently. Morphological variations and the extinction of the Paoha Island fossil assemblage may be associated with changes in the chemistry of Mono Lake since the Pleistocene.

Introduction

The chemistry and biology of Mono Lake, located east of the Sierra Nevada mountain range in eastern California (Figure 1), has undergone many changes since its basin was filled with freshwater after the last Ice Age (Russell 1889). Presently the lake is very alkaline and salty (Gaines 1982). The diatom community of the lake is not diverse, as a single *Nitzschia* species dominates the flora. Historically, however, there was a more diverse and cosmopolitan assemblage in Mono Lake. A portion of the previous diatom assemblage, which is part of the lacustrine record, has been conveniently lifted by volcanic activity to form Paoha Island, one of two islands in the lake. Paoha Island is covered with up to 30 feet of diatomaceous earth. Initial observations indicate fossil diatoms from Paoha Island are different from the present flora and that many teratological forms exist in the fossil material. Since previously published observations on Mono Lake diatoms did not include material from Paoha Island and did not mention the presence of teratological forms (Wornardt 1964; Mason 1967), observations on this material might prove interesting to diatomists.

Materials and Methods

A sample consisting of loose soil, the product of erosion from upper strata, was taken from Paoha Island by Dr. Joe Jehl of Sea World Research. Cleaned diatoms were mounted in Naphrax, and observations and photomicrographs made with an Olympus BHS microscope with Differential Interference Contrast optics. A count of 1000 individuals was made to determine percentages of the various species present in the deposit and percentages

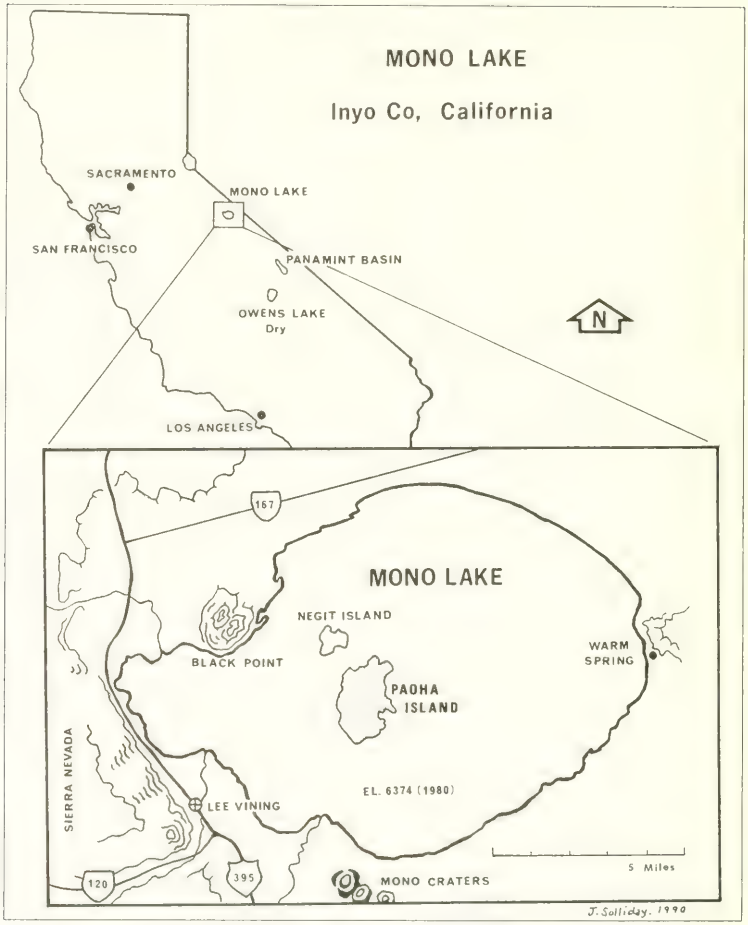


FIGURE 1. Map showing location of Mono Lake and Paoha Island, Inyo County, California.

of teratological forms in the entire community. Percentages of valve types of *Surirella utahensis* were determined from counts of 400 individuals.

Results

The fossil diatom flora of the Paoha Island material is dominated by four species, including *Anomoeoneis costata*, *Surirella utahensis*, *Cyclotella bodanica*, and *S. testudo*. Together these species account for over 92 % of the entire community (Table 1).

TABLE 1. Percentage of individual diatom species composing the Paoha Island fossil assemblage.

Anomoeoneis costata (Kützing) Hustedt	38.0%
Surirella utahensis (Grunow) Hanna et Grant	28.0%
Cyclotella bodanica Grunow	14.7%
Surirella testudo (Ehrenberg) Hanna et Grant	11.7%
Campylodiscus noricus var. *hibernica* (Ehrenberg) Grunow	5.3%
All others	2.3%
	100.0%

Morphological variations within species were obvious upon inspection of the material. To quantify this, three types of morphological variation were identified:

Group 1: — Individuals that are within normal or expected dimensions of a taxon (Figs. 3, 14).

Group 2: — Individuals that are symmetrical but have unfamiliar outlines (Figs. 4–8).

Group 3: — Individuals that are asymmetrical and easily recognized as teratological (Figs. 9–13).

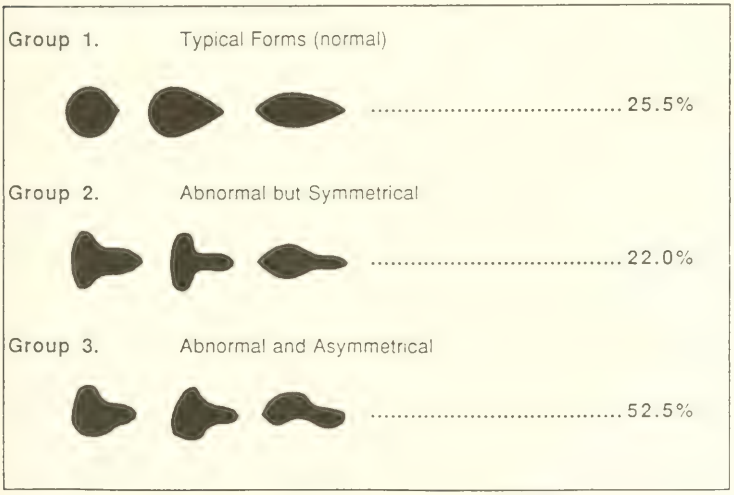


FIGURE 2. Patterns and frequencies of morphological variation observed in *Surirella utahensis*.

In the Paoha Island specimens, only 38 % of the valves were typical (i.e., of Group 1), while 16.5 % were symmetrical but abnormal (Group 2), and 45.5 % were both abnormal and asymmetrical (Group 3). These groupings were applied specifically to valves of *S. utahensis*, which had the largest number of different valve shapes of the Paoha Island taxa. Only 25.5 % of the *S. utahensis* specimens observed exhibited the "typical" morphology of that species, while 22 % were abnormal but symmetrical, and over 50 % were both abnormal and asymmetrical (Fig. 2).

Comments on the four dominant diatom taxa in the Paoha Island material are presented below.

Surirella utahensis (Grunow) Hanna & Grant
(Figs. 3–14)

SYNONYM: *S. ovata* var. *utahensis* Grunow.

One of the most important features for the identification of this taxon is the presence of a transverse fold that occurs in most individuals (Grunow 1875 *in* Schmidt et al.; La Rivers 1978). The fold is normally located about two-thirds up the apical axis from the acute apex (Wornadt 1964). The moderately long, submarginal costae are joined by fine striae that radiate from an indistinct medial line. Striae often radiate to the margin between costae and may be indistinct. Paoha Island specimens range from 60–120 µm in length and 55–110 µm in breadth. Striae number 12–13 in 10 µm, while costae number 3–4 in 10 µm.

Similarities exist among *S. utahensis*, *S. ovalis*, *S. crumena*, and *S. peisonis*. *Surirella ovalis* has been illustrated as being quite diverse morphologically, and many subspecific taxa have been described. Even for the same species it is not unusual to find dissimilar descriptions, evidenced by the illustrations of asymmetrical specimens of *S. ovalis* by Van Heurck (1880–1885, Pl. 73, Fig. 4) and Schmidt et al. (1875, Pl. 24, Fig. 4). This suggests some *Surirella* species are susceptible to variability. Study of the Paoha material indicates that almost no individuals of the same species of *Surirella* can be found to look alike, and that identification of taxa is difficult. The normal morphological variations that occur during the vegetative life cycle are far exceeded and obscured by the high percentage of teratological forms in *S. utahensis*. In *S. ovalis*, smaller specimens usually exhibit abnormalities, but in *S. utahensis* from Paoha Island material it is the larger individuals that showed the greatest degree of variability.

Regarding nomenclature, both Hanna and Grant (1929) and Lohman (1937) regard this diatom as distinct from *S. ovata*, while VanLandingham (1978) considers *S. ovata* var. *utahensis* as a synonym of *S. utahensis*. Given the doubts concerning the type of *S. ovalis* (Krammer and Lange-Bertalot 1987), it seems appropriate to retain the name *S. utahensis*.

Surirella testudo Ehrenberg
(Figs. 19, 20)

This species was the fourth most frequently encountered diatom in the Paoha Island material. It displayed a wide range of teratological forms (e.g., Fig. 20). Mann (1926, p. 53) identified this species from fresh to brackish water and he notes, "This species seems to flourish in water high in mineral content. It often holds its place in lakes that show a gradual increase in salinity after other species have been exterminated by the higher percentage of salts."

There are a number of other *Surirella* species found in very small numbers in the Paoha Island assemblage, including possibly *S. ovalis*, *S. brebissonii*, *S. crumena*, and *S. peisonis*.

Cyclotella bodanica Grunow
(Figs. 15–17)

Cyclotella bodanica was the third most abundant diatom in the Paoha Island assemblage. It has been determined by Håkansson (1986) that slide No. 1016 in the Grunow Collection should be the type for this species. *Cyclotella bodanica* is illustrated in Van Heurck (1880–1885, Pl. 93, Fig. 10) as "*C.* (*comta* var.) *bodanica* Eulenst" from the Bodensee as well as by Schmidt (1901, Pl. 224, Figs. 29–32) and Weber (1971, p. 25, Fig. 15). This species has been reported from San Francisco Bay (Laws 1988) and Utah Lake, Utah (Grimes and Rushforth 1982).

Figures used by Wornardt (1964) to illustrate *C. comta* from Panamint Valley do not conform well with the *Cyclotella* specimens obtained from Paoha Island. Panamint Valley can be geographically associated with Mono Lake and the age of the diatoms are placed within the same time frame. Wornardt illustrates two examples: the first is a small form with a diameter of 19 µm and the other has a diameter of 48 µm. The Paoha Island *Cyclotella* specimens were 35–65 µm in diameter, with a majority of individuals being 55–65 µm. Striae average 11–12 in 10 µm on the valve face and 13–14 in 10 µm at the margins. The examples of Wornardt have irregular patterns of areolae in the central area, whereas the Paoha Island specimens are normally seen with areolae in concentric, radial striae. The disparity between the Panamint specimens of Wornardt and the Paoha Island material may be due to differences in environment, although this cannot be evaluated with any certainty. Wornardt (1964) did not report *C. comta* from Mono Lake in his study.

The Paoha Island specimens of *C. bodanica* fit well into Håkansson's group No. 1 (Håkansson 1986, p. 339), which is represented by *C. bodanica* var. *bodanica* and *C. bodanica* var. *affinis*.

One feature that showed a high degree of variability in *C. bodanica* was the number of rimoprotulae. Rimoportulae numbered from four to 10, with a few specimens having even a higher number (Figures 15, 16). This feature appears in the light microscope as a narrow hyaline finger extending from the edge of the central area halfway into the marginal striae. At the end of this finger is a single opening (rimoprtula). I could find no previous reports of such high numbers of rimoportules in *Cyclotella*. In Hakansson's (1986) study of the *C. comta*/*C. bodanica* complex the highest number of rimoportulae was five, found in *C. bodanica*.

Anomoeoneis costata (Kützing) Hustedt
(Figs. 23–28)

Anomoeoneis costata is the name given this diatom by Wornardt (1964) from the Mono Basin, and it is the most abundant species in the Paoha Island material. It was 110–265 µm in length, 25–55 µm in breadth and marginal striae numbered 12–13 in 10 µm. This diatom is characterized by a distinct row of puncta along the longitudinal axis of the axial area. The transverse striae are often irregular and sometimes staggered at their medial termination. Striae are slightly radiate, and the distal raphe ends are curved in the same direction.

The name *Anomoeoneis* means an "asymmetrical" or "unequal" ship. This asymmetry was in reference to the wall markings. The unornamented central area runs from the center of the valve all the way to the margin, but on the opposite side the central area extends only halfway to the margin. Irregular punctation on either side of the axial area is also evident in this taxon. Regarding outline, Patrick and Reimer (1966) state that only a few

forms of *Anomoeoneis* have ever been seen with a central constriction, but this feature has not been reported for *A. costata*. In the Paoha Island material this taxon exhibited a central constriction or was panduriform in outline (Figs. 26, 27). In fact, in the discussion of this species, Patrick and Reimer (1966, p. 376) note the larger specimens of *A. costata* are gibbous at the center of the valve. As for the *Anomoeoneis* specimens from Paoha Island, they consistently express a curious diversity of morphological shapes, including a fair number (approximately 2 % of the total number of *Anomoeoneis* specimens observed) that are panduriform. I am not certain the panduriform specimens represent teratologies or a previously undescribed variety of *A. costata*.

Anomoeoneis is an important genus for those workers studying highly saline inland waters. Hanna (1932) and Patrick and Reimer (1966) state *A. costata* is a definite indicator of more or less saline waters, while Boyer (1927) reported this taxon from the Gulf of California and considered it characteristic of brackish waters. As for the age of this species, Lohman (1937) identified *Anomoeoneis* from Pleistocene deposits in Harney County, Oregon, and neither *A. sphaerophora* nor *A. costata* are probably older than Pliocene age.

Because of the similarity of Mono Lake and certain lakes in East Africa, *Anomoeoneis* populations can be compared to estimate similarity of ecological parameters of these widely separated systems. Gasse (1986) indicated *Anomoeoneis* species were found typically in habitats of pH 8.5–9.5. This genus is considered a good indicator of medium to high conductivity and alkalinity, and its best development often occurs in waters of high mineral content. Elevated temperatures apparently do not inhibit the growth of *A. costata*.

Discussion

Today, Mono Lake's diatom community consists primarily of a small species of the genus *Nitzschia*. Occasionally a few other hardy species can be found, including a curious, featureless diatom that slowly glides across the field of the microscope, possibly associated with *Anomoeoneis*. For over 700,000 years diatoms have been living and depositing their frustules on the muddy bottom of the lake. Only an exhaustive study of the complete column of Mono Lake sediments could reveal how often populations of diatoms have been introduced and later exterminated through the lake's geological evolution. The diatoms observed in this study were probably among the final generations of the lake's later shift from fresh to saline waters. Influence of other environmental conditions, such as temperature and total desiccation, never became a factor; the Paoha Island diatoms are suggested to be temperature-tolerant and Mono Lake has never dried up. An explanation of the causes of the teratologies described herein is beyond the scope of this study, however, alterations in the lake's chemistry certainly may have been influential in causing the morphological variation and anomalies observed. The Paoha Island deposit represents a window that allows us to look back into a natural experiment in diatom tolerance and potential life cycle strategies and into a record of extinction of a long-standing diatom assemblage.

Acknowledgements

Several people provided assistance with the taxonomy, methods, and supply of samples for this study. William Sokol afforded me a great deal of encouragement, as well as my initial training in techniques vital to this work. He also has been a source of many valuable samples and important, hard-to-find literature. Joe Jehl of Sea World Research, San Diego, California, kindly provided the Paoha Island sample. Important references and guidance were contributed by Jeff Johansen of John Carroll University. Constructive criticism was provided by the following authorities: John Carter, Robert McLaughlin, Victor Porguen,

and Ed Theriot.

Literature Cited

BOYER, C. 1927. Synopsis of North American Diatomaceae. Part II. Naviculatae, Surirellatae. Proc. Acad. Nat. Sci. Phila. 79, Suppl. Pp. 229–583.

GAINES, D. 1982. Mono Lake Guidebook. Mono Lake Committee, Kutsavi Books, Lee Vining, California.

GASSE, F. 1986. East African diatoms. Taxonomy, ecological distribution. Bibl. Diatomologica 11:1–201.

GRIMES, J. AND S. RUSHFORTH. 1982. Diatoms of Recent bottom sediments of Utah Lake, U. S. A. Bibl. Phycologica 55:1–179.

HÅKANSSON, H. 1986. A study of species belonging to the *Cyclotella bodanica/comta* complex (Bacillariophyceae). Pp. 329–354 *in* Proceedings of the Ninth International Diatom Symposium. F. E. Round.

HANNA, G. D. AND W. M. GRANT. 1929. Brackish-water Pliocene diatoms from the Etchgonian Formation of central California. J. Paleontol. 3:87–101.

———. 1932. Diatoms of Pyramid Lake, Nevada. Trans. Am. Microsc. Soc. 50:281–297.

KRAMMER, K. AND H. LANGE-BERTALOT. 1987. Morphology and taxonomy of *Surirella ovalis* and related taxa. Diatom Res. 2:77–95.

LA RIVERS, I. 1978. Algae of the western Great Basin. Bioresources Center, Desert Research Institute, Publication No. 50008. University of Nevada.

LAWS, R. 1988. Diatoms (Bacillariophyceae) from surface sediments in the San Francisco Bay estuary. Proc. Calif. Acad. Sci. 45:133–254.

LOHMAN, K. E. 1937. Pliocene diatoms from the Kettleman Hills, California. U. S. G. S. Prof. Pap. 189-C:81–102.

MASON, D. T. 1967. Limnology of Mono Lake, California. Univ. Calif. Publ. Zool. 83:1–110.

PATRICK, R. M. AND C. W. REIMER. 1966. The Diatoms of the United States. Vol. 1. Acad. Nat. Sci. Phila. Monogr. No. 13. 688 pp.

RUSSELL, I. C. 1889. Quaternary history of the Mono Lake Valley, California. Pp. 261–394 *in* J. W. Powell, Eighth Annual Report of the United States Geological Survey, Part 1. U. S. Govt. Print. Off. Washington, D. C.

SCHMIDT, A., ET AL. 1874–1959. Atlas der Diatomaceen-Kunde. Heft 1–120, Tafeln 1–480. R. Reisland, Leipzig.

VAN HEURCK, H. 1880–1885. Synopsis des Diatomées de Belgique. Atlas. Plates 1–132. Ducaju et Cie, Anvers.

VANLANDINGHAM, S. L. 1978. Catalogue of the Fossil and Recent Genera and Species of Diatoms and their Synonyms. Part VII. *Rhoicosphenia* through *Zygoceros*. Pp. 3603–4241. J. Cramer, Lehre.

WEBER, C. I. 1971. A Guide to the Common Diatoms at Water Pollution Surveillance State Stations. U. S. E. P. A., U. S. Govt. Print. Off. Washington, D. C. 101 pp.

WORNARDT, W. W., Jr. 1964. Pleistocene diatoms from Mono and Panamint Lake Basins, California. Occ. Pap. Calif. Acad. Sci. 46:1–27.

Explanation of Plates

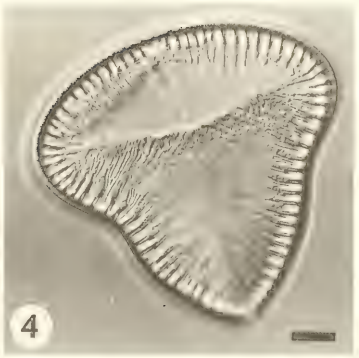
Plate 1, Figures 3–8
FIGURES 3–8. *Surirella utahensis*. FIGURE 3. Typical form. FIGURES 4–8. Symmetrical but abnormal forms. Scale bars = 10 μm.

Plate 2, Figures 9–14
FIGURES 9–14. *Surirella utahensis*. FIGURES 9–13. Teratological forms, asymmetrical and abnormal outlines. Note that in Figure 13 the curved fold is to the bottom or the cuneate apex. FIGURE 14. Specimen with curved fold to the top or more rounded apex. Scale bars = 10 μm.

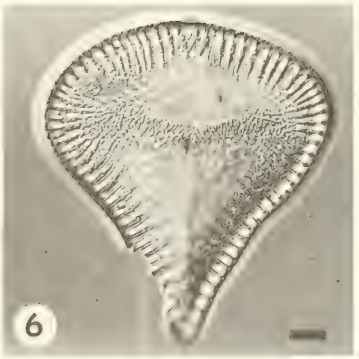
Plate 3, Figures 15–20
FIGURES 15–17. *Cyclotella bodanica*. FIGURE 15. Note shadow image of rimoportulae within marginal striae. FIGURE 16. Specimen with 10 rimoportulae. FIGURE 17. Detail of marginal costae showing placement of fultoportulae (appear as small white dots at the base of heavier costae). FIGURE 18. Unknown teratological form. FIGURES 19, 20. *Surirella testudo*. Figure 20 shows a teratological form with striae radiating from a central aberration. Scale bars = 10 μm.

Plate 4, Figures 21–28
FIGURES 21–28. FIGURE 21. *Surirella testudo* with a valve of *Cocconeis placentula* on it. FIGURE 22. *Campylodiscus clypeus*. FIGURES 23–28. *Anomoeoneis costata* showing different types of outline. Scale bars = 10 μm.

3


4

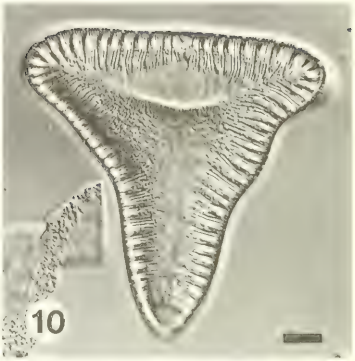
5

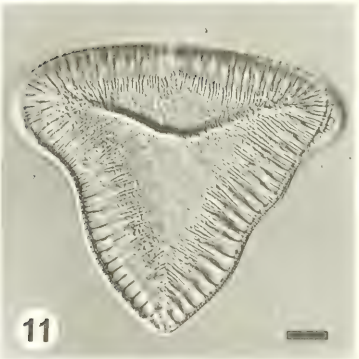

6

7

8

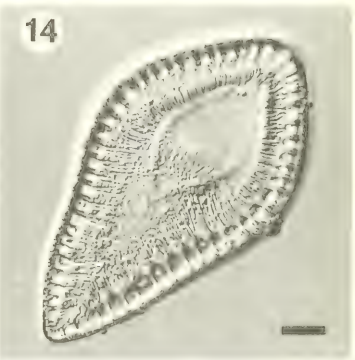
9

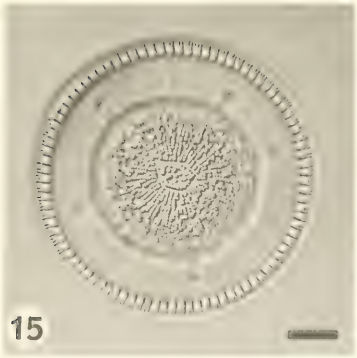

10

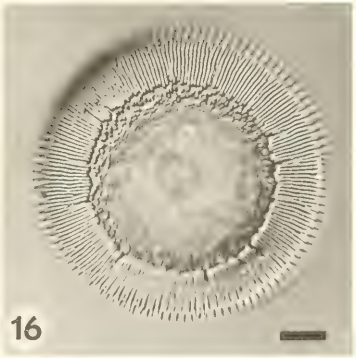

11

12

13


14


15


16

17

18

19

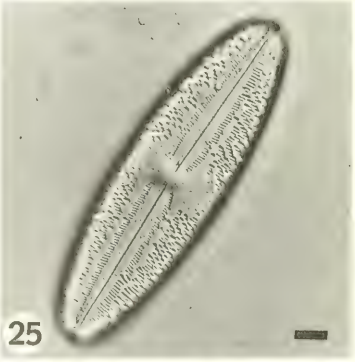
20

21

22

23

24


25

26

27

28

Lagoonal Diatom Flora of the Holocene Baltic Litorina Sea in Comparison with the Eemian Baltic Sea Flora

by

Tuulikki Grönlund

Geological Survey of Finland, Betonimiehenkuja 4,
FIN-02150 Espoo, Finland

with 4 figures

Abstract:: As a consequence of land uplift and varying connections to the Atlantic Ocean, the conditions of the Baltic Sea, now a typical brackish water basin, have shifted in the course of its history between freshwater, brackish, and marine. Earlier in the Baltic basin there were two sea phases that were more extensive and more saline than the recent one. They are the Baltic Litorina Sea that occurred about 7,500–3,000 years ago during the Holocene epoch and the Eemian Baltic Sea that occurred during the Eemian interglacial stage (120,000 years ago). The Baltic Litorina Sea was characterized by the so-called *Clypeus* flora. The most characteristic species of that flora are *Campylodiscus clypeus* Ehrenberg, *Anomoeoneis sphaerophora* var. *sphaerophora* (Ehrenberg) Pfitzer, *A. sphaerophora* var. *sculpta* (Ehrenberg) O. Müller, *Amphora robusta* Gregory, *Nitzschia circumsuta* (J. W. Bailey) Grunow, *N. scalaris* (Ehrenberg) W. Smith, and *Surirella striatula* Turpin. The *Clypeus* flora reflects the presence of a shallow lagoon of the Holocene Baltic Litorina Sea, just before the isolation of the lake basins from the sea. Sediments of the Eemian Baltic Sea have been found mainly in the western part of Finland. The history of the sea is still fragmentarily known. A *Clypeus* flora closely similar to the Holocene assemblage was recently identified from Eemian sediment sequences from Norinkylä at Teuva, western Finland, consisting of *Campylodiscus clypeus*, *Nitzschia scalaris* and *Diploneis smithii* (Brébisson) Cleve. Shore displacement and development from the sea to a freshwater basin may have taken place in a surprisingly similar manner, although the submergence during the Eemian interglacial stage was greater than during the Holocene.

Introduction

The late and postglacial (Late Weichselian and Holocene) phases of the Baltic Sea have been studied extensively (e.g., Backman and Cleve-Euler 1922; Backman 1937; Mölder 1943; Florin 1946, 1957; Cleve-Euler 1951–55; Simonsen 1962; Mölder and Tynni 1967–73; Alhonen 1971; Eronen 1974; Tynni 1975–80; Miller and Robertsson 1979; Hyvärinen 1984) and the Holocene history of the sea is well known. As a consequence of land uplift and varying connections to the Atlantic Ocean, the salinity status of the Baltic Sea has alternated between freshwater, brackish and marine during the postglacial period. Rather little is known about the development of the Baltic Sea basin before the last glaciation. Some recent finds, especially from Finnish Ostrobothnia and in the southern part of the

FIGURE 1. The recent Baltic Sea with simplified surface isohalines (‰).

Baltic Sea, in Estonia, have provided new data on the Eemian marine phases in the Baltic basin.

The Baltic Sea is now a typical brackish water basin. The salinity of the sea varies from 8 to less than 3 ‰ (Fig. 1). Hustedt (1957) indicates that the pleioeuryhaline polyhalobous and β-mesohalobous diatoms thrive best in this kind of water.

In the Baltic basin, two more extensive sea phases have been identified, with higher salinities than the recent one. About 7,500–3,000 years ago during the Holocene epoch the basin was occupied by the Baltic Litorina Sea (Fig. 2) and before the last glaciation around 125,000 years ago during the Eemian interglacial stage the basin was filled by the Eemian Baltic Sea (Fig. 3). Due to the land uplift, sediments of the Baltic Litorina and the Eemian Baltic Seas now can be discovered in coastal land areas well above the present level of the Baltic Sea.

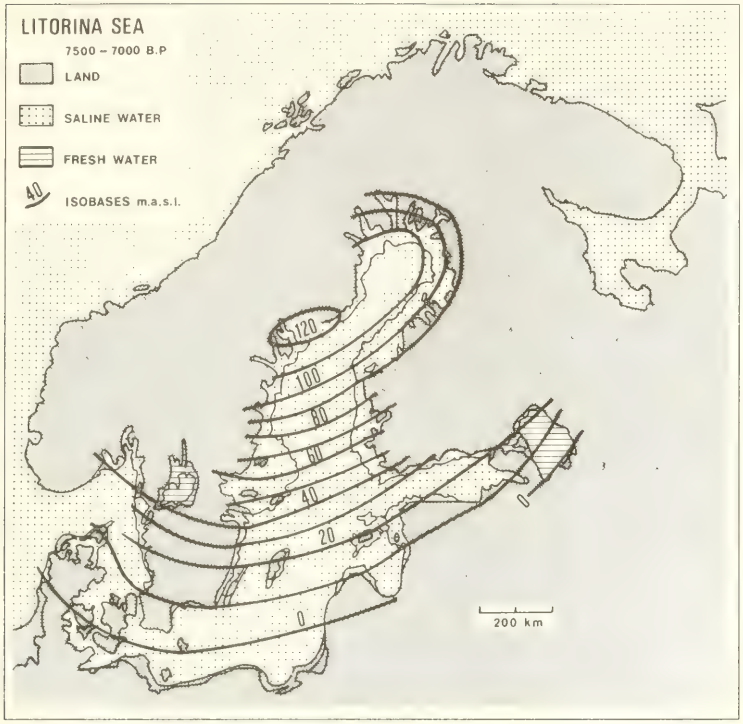


FIGURE 2. The Baltic Litorina Sea about 7,500 years ago, during the Holocene (after Donner and Eronen 1981).

THE BALTIC LITORINA SEA

The diatom flora of the Baltic Litorina Sea is well known. It is to some extent different in the pelagic phase as compared to the coastal area of the sea. Diatoms representing the deep water facies include *Actinocyclus octonarius* Ehrenberg (syn. *A. ehrenbergii* Ralfs), *Chaetoceros mitra* (J. W. Bailey) Cleve, *C. subsecundus* (Grunow) Hustedt, *Thalassiosira hyperborea* var. *pelagica* (Cleve-Euler) Hasle, and *T. hyperborea* var. *lacunosa* (Berg) Hasle (which were previously named as *Coscinodiscus lacustris* Grunow and *C. lacustris* var. *hyberborea* Hustedt and var. *septentrionalis* Grunow, cf. Hasle and Lange 1989), *Rhizosolenia calcar avis* Schultze, *Thalassionema nitzschioides* Grunow, and *Thalassiosira baltica* (Grunow) Ostenfeld. Diatoms from the coastal areas are *Cocconeis scutellum* Ehrenberg, *Diploneis didyma* (Ehrenberg) Cleve, *D. interrupta* (Kützing) Cleve, *Grammatophora oceanica* Grunow, *Hyalodiscus scoticus* (Kützing) Grunow, *Navicula peregrina* (Ehrenberg) Kützing, *Nitzshia punctata* (W. Smith) Grunow, *N. tryblionella* Hantzsch, and *Rhabdonema arcuatum* (Lyngbye) Kützing. From coastal areas of the Baltic Litorina

Sea the so-called *Clypeus* flora is present (e.g., Halden 1916; Florin 1946). The name comes from the dominant species of this flora, *Campylodiscus clypeus* Ehrenberg. The accompanying species are *Amphora robusta* Gregory (named also as *A. mexicana* var. *major* (Cleve) A. Cleve), *Anomoeoneis sphaerophora* var. *sphaerophora* (Ehrenberg) Pfitzer, *A. sphaerophora* var. *sculpta* (Ehrenberg) O. Müller, *Nitzschia circumsuta* (J. W. Bailey) Grunow, *N. scalaris* (Ehrenberg) W. Smith, *N. tryblionella* and *Surirella striatula* Turpin. This flora forms the part of the diatom succession related to sheltered coastal bays and is not found in the deep water facies. In Finland the flora is found especially on the southern and southwestern coasts, but in Ostrobothnia western Finland it is not so common (Eronen 1974). The *Clypeus* flora reflects the existence of a shallow lagoon preceding the emergence of the site as a result of isostatic land uplift. The term "lagoonal flora" also refers to this environment.

The Eemian Baltic Sea

Diatoms of the Eemian Baltic Sea have been encountered at several localities but, unfortunately, they are usually as redeposited and/or mixed in with freshwater diatom species (Brander 1937, 1943; Tynni 1971; Miller and Persson 1973; Niemelä and Tynni 1979). A fully marine diatom flora has been found so far from three sites: on the island of Suur-Prangli in the southern Gulf of Finland, in Estonia (Liivrand 1984, 1987), Evijärvi (Eriksson et al. 1980) and Ollala (Forsström et al. 1987, 1988; Grönlund 1988) from Ostrobothnia, Finland. On this basis, the history of the sea is still only fragmentarily known. It is evident that the Eemian Baltic Sea covered a more extensive area and had a clearly higher salinity than the Baltic Litorina Sea, which again was larger and more saline than the Baltic Sea of today. A relatively broad connection must have existed between the Baltic Basin and the Atlantic Ocean for a considerable period of time. There was very probably also a connection between the Baltic and the White Sea via Karelia at that time (Zans 1936; Niemelä and Tynni 1979).

The marine stage proper of the Eemian Baltic Sea is characterized by an abundant diatom flora. Littoral diatoms, such as *Grammatophora oceanica, Hyalodiscus scoticus,* and *Paralia sulcata* (Ehrenberg) Cleve, dominate and true plankton species are almost totally absent. The diatom flora also includes many diatoms that mainly thrive in highly saline water and are not found earlier in the Finnish area, such as *Amphora acuta* Gregory, *A. crassa* var. *punctata* A. Schmidt, *Diploneis notabilis* (Greville) Cleve, *D. mediterranea* (Grunow) Cleve, and *Navicula arenaria* Donkin. Some of the diatoms present thrive in warm water (e.g., *Diploneis mediterranea* and *D. papula* (A. Schmidt) Cleve (Cleve-Euler 1940) but there are also species present that prefer cold water, such as *Campylodiscus angularis* Gregory, *Grammatophora arcuata* Ehrenberg, *Navicula glacialis* (Cleve) Grunow, and *Trachyneis aspera* (Ehrenberg) Cleve (Cleve-Euler 1940).

The Norinkylä Site

New information about the Eemian Baltic Sea has now been obtained from the Norinkylä site at Teuva in Finnish Ostrobothnia (Fig. 3). The sequence at Norinkylä is situated in a narrow esker extending from north to south, and it was first studied by Niemelä and Tynni (1979). New samples below the mire on the western side of the esker were taken using a percussion drill with a flow-through bit sampler. The samples were first bleached with diluted H_2O_2 for 24 h at 50°C, and then subjected to repeated suspensions and decantations. Material was mounted in Hyrax, which has a refractive index of 1.65. Whenever possible 500 diatom valves were identified from each sample depth.

FIGURE 3. The northern part of the Eemian Baltic Sea before the last glaciation more than 100,000 years ago, during the Eemian interglacial stage. The main Eemian marine sites in Finland and in Estonia are marked in the figure.

In Figure 4 one of the new profiles is presented. The profile underlying the till deposits could not be sampled continuously but it was possible to discern the following diatom succession. The sediment consists of silt and gyttja silt. The bottom part of the profile contains diatoms of the Eemian Baltic Sea proper. Above 8 m depth in the profile, the diatom flora changes radically, and species typical of brackish waters dominate. The characteristic species include *Campylodiscus clypeus*, *Nitzschia scalaris*, and *Diploneis smithii* (Brébisson) Cleve, in other words the same species that belong to the *Clypeus* flora of the Baltic Litorina Sea. The *Clypeus* flora species are clearly dominant in a 30 cm sequence of this Norinkylä profile. In the sequence containing *Clypeus* flora species, high values of *Corylus* pollen (ca. 20%) were found (Brita Eriksson, pers. comm. 1990). Pollen of this type indicates the time of the Eemian climate optimum. *Corylus* was clearly less frequent during the Holocene in Ostrobothnia (Donner 1964; Niemelä and Tynni 1979).

During the Holocene this diatom assemblage is considered to reflect a lagoonal situation before the isolation from the sea. The same situation is also seen in the Norinkylä profile. Isolation from the Eemian Baltic Sea begins in the sediments about at the depth of 6.80 m. The present elevation of the site is ca 103 m a.s.l. (110–6.8 m) compared to highest Holocene Baltic Litorina Sea of 80 m a.s.l.

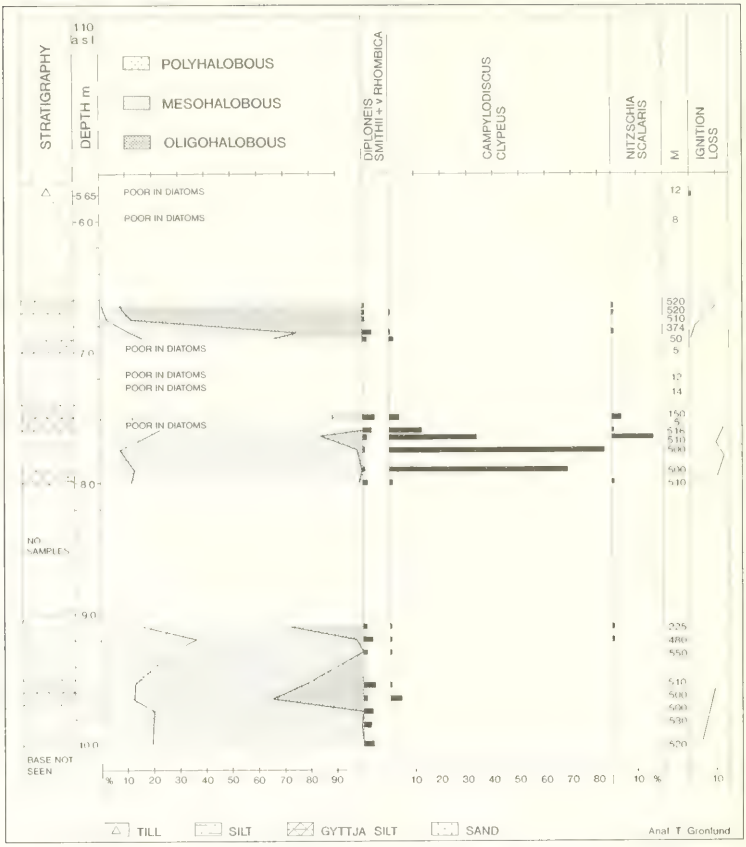


FIGURE 4. The diatom diagram from the Eemian deposits from Norinkylä, at Teuva. The diatoms belonging to the *Clypeus* flora are shown separately.

CONCLUSIONS

The *Clypeus* flora, with some characteristic diatom species corresponding to a shallow lagoon of the Baltic Litorina Sea, is present in many localities from coastal areas of the Baltic basin both in Sweden and Finland. This typical flora represents a change from open Baltic Litorina bay to a sheltered, independent lake basin. The end of this lagoonal period thus marks the emergence of the site.

The first occurrence of *Clypeus* flora has been connected with the highest raised shoreline of the Baltic Litorina Sea, especially in the northern part of the Baltic basin where land uplift has been rapid. It is present in lagoonal sediment between the highest Litorina limit and the present Baltic Sea.

The *Clypeus* flora is now found in the Eemian Baltic Sea sediments from the Norinkylä site at Teuva, Finland. The typical *Clypeus* flora follows the rich marine diatom flora of the Eemian Baltic Sea in the diatom succession of the Norinkylä profile. The *Clypeus* flora at the Norinkylä site also reflects the development from moderately deep marine water basin to shallow littoral bay and finally to a freshwater basin in the similar way that has been described from Holocene sites (Donner 1964).

Although data from the Eemian *Clypeus* flora are scarce, the *Clypeus* floras found in sediments from these two seas appear to be quite similar. Development from the sea to a fresh water basin may have taken place in a surprisingly similar way, although there is a difference in timing of more than 100,000 years.

Acknowledgements

I wish to thank Prof. Urve Miller for critically reading the manuscript and her valuable comments on the subject.

Literature Cited

ALHONEN, P. 1971. The stages of the Baltic Sea as indicated by the diatom stratigraphy. Acta Bot. Fenn. 92: 1–18.

BACKMAN, A. L. 1937. Om Litorinagränsen i Haapavesi och Diatomacéfloran på Suomenselkä. Acta Soc. Fauna Flora Fenn. 60:209–244.

BACKMAN, A. L. AND A. CLEVE-EULER. 1922. Die fossile Diatomeenflora in Österbotten. Acta Forest. Fenn. 22:1–74.

BRANDER, G. 1937. Ein Interglazialfund bei Rouhiala in Südostfinnland. Bull. Comm. Géol. Finlande 118:1–76.

———. 1943. Neue Beiträge zur Kenntnis der interglazialen Bildungen in Finland. Bull. Comm. Géol. Finlande 128:87–137.

CLEVE-EULER, A. 1940. Das letztinterglaziale Baltikum und die Diatomeenanalyse. Beih. Bot. Centralbl. LX, B, 3:287–334.

———. 1951. Die Diatomeen von Schweden und Finnland. I. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 2:1–163.

———. 1952. Die Diatomeen von Schweden und Finnland. V. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 3:1–153.

———. 1953. Die Diatomeen von Schweden und Finnland. II. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 4:1–158.

———. 1953a. Die Diatomeen von Schweden und Finnland. III. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 5:1–225.

———. 1955. Die Diatomeen von Schweden und Finnland. IV. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 5:1–232.

DONNER, J. 1964. The late-glacial and post-glacial emergence of south-western Finland. Soc. Sci. Fenn. Comm. Phys.-Math. 30:1–47.

DONNER, J. AND M. ERONEN. 1981. Stages of the Baltic Sea and Late Quaternary shoreline displacement in Finland. Excursion Guide, INQUA subcommission of shorelines of northwestern Europe. University of Helsinki, Department of Geology, Division of Geology and Palaeontology, Stencil, No. 5:1–53.

ERIKSSON, B., T. GRÖNLUND, AND R. KUJANSUU. 1980. Interglasiaalikerrostuma Evijärvellä, Pohjanmaalla. Summary: An interglacial deposit at Evijärvi in the Pohjanmaa region, Finland. Geologi 32: 65–71.

ERONEN, M. 1974. The history of the Litorina Sea and associated Holocene events. Soc. Sci. Fenn. Comm. Phys.-Math. 44:1–195.

FLORIN, M.-B. 1946. *Clypeus*floran i postglaciala fornsjölagerföljder i östra Mellansverige. Geol. Fören. Stockholm Förhandl. 68:429–438.

———. 1957. Plankton of fresh and brackish waters in the Södertälje area. Acta Phytogeogr. Suecica, 37:1–144.

FORSSTRÖM, L., M. ERONEN, AND T. GRÖNLUND. 1987. On marine phases and shore levels of the Eemian interglacial and Weichselian interstadials on the coast of Ostrobothnia, Finland. Geol. Surv. Finland Spec. Pap. 2:37–42.

FORSSTRÖM, L., M. AALTO, M. ERONEN, AND T. GRÖNLUND. 1988. Stratigraphic evidence for Eemian crustal movements and relative sea-level changes in Eastern Fennoscandia. Palaeogeogr. Palaeoclimat. Palaeoecol. 68:317–335.

GRÖNLUND, T. 1988. The diatom flora of the Eemian deposit at Haapavesi, western Finland. Geol. Surv. Finland, Rept. Invest. 79:1-14.

HALDEN, B. 1916. Försök till bestämning av Litorinagränsen i Hälsingland. Geol. Fören. Förhandl. 38: 224–225.

HASLE, G. R. AND C. B. LANGE. 1989. Freshwater and brackish water *Thalassiosira* (Bacillariophyceae): taxa with tangentially undulated valves. Phycologia 28:120–135.

HUSTEDT, F. 1957. Die Diatomeenflora des Flussystems der Weser im Gebiet der Hansestadt Bremen. Abh. Naturwiss. Bremen 34:181–440.

HYVÄRINEN, H. 1984. The *Mastogloia* stage in the Baltic Sea history: Diatom evidence from southern Finland. Bull. Geol. Soc. Finland 56:99–115.

LIIVRAND, E. 1984. The Interglacials of Estonia. Ann. Acad. Sci. Fenn. A. III. 138: 1–16.

———. 1987 Regional type section of the Eemian marine deposits on Suur-Prangli. Proc. Acad. Sci. Estonian SSR. Geology 36:20–26.

MILLER, U., AND C. PERSSON. 1973. A lump of clay embedded in glacial intermoraine sand. Geol. Fören. Stockholm Förhandl. 95:342–246.

MILLER, U., AND A.-M. ROBERTSSON. 1979. Biostratigraphical investigations in the Anundsjö region, Ångermanland, northern Sweden. Early Norrland, 12:1–76.

MÖLDER, K. 1943 Studien über die Ökologie und Geologie der Bodendiatomeen in der Pojo-Bucht. Ann. Bot. Soc. Zool.-Bot. Fenn. Van. 18:1–202.

MÖLDER, K., AND R. TYNNI. 1967. Über Finnlands rezente und subfossile Diatomeen I. C. R. Soc. Géol. Finlande 39:199–217.

———. 1968. Über Finnlands rezente und subfossile Diatomeen II. Bull. Geol. Soc. Finland 40:151–170.

———. 1969. Über Finnlands rezente und subfossile Diatomeen III. Bull. Geol. Soc. Finland 41:235–251.

———. 1970. Über Finnlands rezente und subfossile Diatomeen IV. Bull. Geol. Soc. Finland 42:129–144.

———. 1971. Über Finnlands rezente und subfossile Diatomeen V. Bull. Geol. Soc. Finland 43:203–220.

———. 1972. Über Finnlands rezente und subfossile Diatomeen VI. Bull. Geol. Soc. Finland 44:141–159.

———. 1973. Über Finnlands rezente und subfossile Diatomeen VII. Bull. Geol. Soc. Finland 45:159–179.

NIEMELÄ, J. AND R. TYNNI. 1979. Interglacial and interstadial sediments in the Pohjanmaa region, Finland. Geol. Surv. Finland, Bull. 302:1–48.

SIMONSEN, R. 1962. Untersuchungen zur Systematik und Ökologie der Bodendiatomeen der westlichen Ostsee. Int. Rev. Ges. Hydrobiol. Syst. Beih. I. Berlin. 1–144..

TYNNI, R. 1971. The diatoms in the Somero clay. In Redeposited Eemian marine clay in Somero, south-western Finland. In J. Donner and R. Gardemeister, eds. Bull. Geol. Soc. Finland 43:851987.

———.1975. Über Finnlands rezente und subfossile Diatomeen, VIII. Geol. Surv. Finland Bull. 274:1–55.

———. 1976. Über Finnlands rezente und subfossile Diatomeen, IX. Geol. Surv. Finland Bull. 284:1–371.

———. 1978. Über Finnlands rezente und subfossile Diatomeen, X. Geol. Surv. Finland Bull. 296:1–55.

———. 1980. Über Finnlands rezente und subfossile Diatomeen, XI. Geol. Surv. Finland Bull. 312:1–93.

ZANZ, V. 1936. Das letzinterglaziale Portlandia-meer des Baltikums. Bull. Comm. Géol. Finlande 115:231–250.

Marine Pleistocene Diatom Assemblages of Northeastern Europe

by

Emma Loseva

Komi Scientific Center, Ural Department,
Academy of Sciences of Russia, Syktyvkar, 167610, Russia

with 2 figures, 1 table, and 3 plates

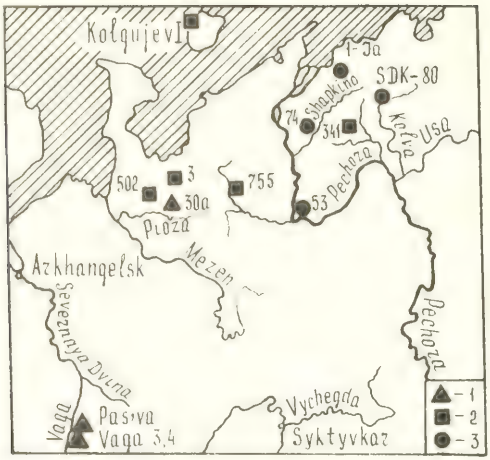
Abstract: The marine Pleistocene diatom assemblages of northeastern Europe contain nearly 560 species and varieties, about 480 of which are Quaternary and 80 (together with Silicoflagellatae) are ancient (late Cretaceous-Paleogene) redeposited forms. All species are neritic or littoral and correspond as a whole to one diatom zone of the North Atlantic—the *Thalassiosira oestrupii* zone. The assemblages are divided into three age groups: early Pleistocene (Günz-Mindel, more than 600 Kyr), middle Pleistocene (Riss 1–2, 180–130 Kyr) and late Pleistocene (Riss-Würm, 110–80 Kyr). The most distinct boundary is between upper and middle Pleistocene diatom assemblages.

Introduction

Several thousand samples from a number of exposed sections and cores in northeastern Europe were examined. Most of them were collected by the author in field expeditions over many years; some were received from other organizations. The observations were carried out with the help of light, transmission, and scanning electron microscopy (LM, TEM, and SEM, respectively). The stratigraphic position of these samples is considered in light of the diatom assemblages.

Diatom Assemblages

The stratigraphic scheme of Pleistocene deposits of the region (Guslitzer, Loseva et al., 1986) has been worked out on a climatic-stratigraphic basis, i.e., on glacial-interglacial cycles. We have distinguished 14 horizons that are comparable with the horizons of the Inter-regional Quaternary stratigraphic scheme of the East-European Platform for the period of 0–0.8 m.y. Marine and freshwater diatom assemblages were found only in the interglacial sediments. The marine assemblages are important for the determination of sediment age. Diatoms were found in three different horizons (Loseva, 1992): early Pleistocene kolvinskaja suite (Günz-Mindel, more than 600 Kyr), middle Pleistocene shklovskij horizon (Riss 1–2, 180–130 Kyr), and upper Pleistocene mikulinskij horizon (Riss-Würm, 110–80 Kyr). The early Pleistocene assemblages are known in the eastern part of the region in the Bolshezemelskaja tundra, the middle Pleistocene assemblages are from the Bolshezemelskaja tundra to northeastern Pritimanje, and the upper Pleistocene assemblages occur in the western part of the region, in the Pioza and Vaga river basins (Figs. 1, 2).



TEXTFIGURE 1. Location of bore-holes and sections with diatom assemblages: 1—mikulinskij horison (Q_3), 2—shklovskij horison (Q_2), 3—kolvinskaja suite (Q_1).

EARLY PLEISTOCENE DIATOM ASSEMBLAGES

The early Pleistocene marine diatom assemblages were studied in four base sections (SDK-80, 74, 1-Ja and 53 bore-holes). The assemblage in bore-hole SDK-80 (in the centre of Bolshezemelskaja tundra) reflects marine littoral conditions. *Paralia sulcata* dominates, *Hyalodiscus obsoletus*, *Actinocyclus curvatulus*, *A. ochotoensis*, *A. divisus*, *Actinoptychus senarius*, and *Navicula distans* are present consistently. There are few pelagic-planktonic species.

The assemblage in bore-hole 74 (in the western part of Bolshezemelskaja tundra) is more abundant and contains more deep-water species. *Paralia sulcata*, *Thalassiosira antarctica*, *A. curvatulus*, *A. ochotoensis*, *N. distans* are characteristic taxa of this assemblage. Planktonic species make up about 90 % of the assemblage, of which *Thalassiosira* specimens account for a half.

A still more abundant and diverse diatom assemblage was found in bore-hole 1-Ja (in the northern part of the Pechora lowland). *Paralia sulcata* dominates (75–96% of marine specimens). *Thalassiosira nidulus*, *Rhaphoneis rhombica*, *Rhizosolenia curvirostris*, *Thalassionema nitzschioides* are common in the material. The proportion of planktonic specimens is, however, not great. *Thalassiosira* specimens make up only 6% of the assemblage. The littoral diatom assemblage from bore-hole 53 (south of 1-Ja, also in Pechora River valley) was included in the same group. It is poor in quantity and quality. *Paralia sulcata* dominates in this deposit. There are littoral planktonic species, but the pelagic-planktonic ones are practically absent, including species characteristic of other sections.

In order to determine sediment age in these sections the geological and hypsometrical conditions, as well as results of other analyses, were evaluated. First and foremost of these was palynology, but peculiarities of the diatom assemblages proper were taken into account, in particular, the presence of *T. nidulus*, *A. divisus*, *A. ochotoensis*, and *R. cur-*

Fig. 2. Correlation of bore-holes and sections with diatom assemblages: 1, soil; 2, sand; 3, pebbles and boulders; 4, 5, sandclay; 6, aleurite; 7, clay; 8, till; 9, scree; 10, mollusc shells; 11, intervals with diatom assemblages; 12, from mikulinskij horizon; 13, from shklovskij horizon; 14, from kolvinskaja suite.

virostris. In all four assemblages, 260 species and varieties of diatoms and Silicoflagellatae were registered (Table 1), including about 200 Quaternary taxa. Of this group, 74% are marine species and 26% freshwater ones. *Paralia sulcata* is the most abundant and constant. *Thalassiosira baltica*, *H. obsoletus*, *A. curvatulus A. octonarius*, *R. rhombica*, *Chaetoceros mitra*, *Rhizosolenia hebetata f. hiemalis*, *Grammatophara anagulosa*, *G. arctica*, *N. distans*, *Diploneis incurvata*, *D. interrupta*, *D. smithii*, *Sciolopleura tumida*, *Cocconeis costata*, *Amphora proteus*, *Catenula adhaerens*, and *Rhopalodia gibberula* also are present in all sections. The genera *Thalassiosira* (15 species), *Diploneis* (14) *Cocconeis* (14) and *Navicula* (12) are the most varied. The characteristic species from Kolvinskaja suite are shown in Plate 1.

Middle Pleistocene Diatom Assemblages

The middle Pleistocene marine diatom assemblages have been studied in four sections. The assemblage in bore-hole 341 (in the western Bolshzemelskaja tundra) is by far more varied than any of the early Pleistocene ones: more than 200 Quaternary species. The assemblage is littoral. *Paralia sulcata*, *Thalassiosira* aff. *parva*, *T. antarctica*, *T. bramaputrae* var. *septentrionalis*, *T.* aff. *levandery*, *A. selarius*, *Chaetoceros holsaticus*, *C. mitra*, and *Delphineis surirella* dominate. Of the age-determinative species, *T. nidulus* is present. There are some newly described species, including *Cyclotella bisymmetrica* Loss., *Cistula lopenziana* var. *punctata* Loss., and *Navicula spuma* var. *minor* Loss. In section 755 (in Middle Timan) the diatom assemblage is less varied and abundant than in bore-hole 341. *Paralia sulcata*, *A. senarius*, and *N. distans* dominate. *Hyalodiscus obsoletus*, *R. rhombica*, and *T. nitzschioides* are consisently present. The assemblage is neratic. Of the age-determinative species, *T. nidulus*, *A. ochotoensis*, and valve fragments of *R. curvirostris* are noted.

Two middle Pleistocene Diatom assemblages from northeastern Pritimanje have beel studied. In bore-hole 502 a very abundant (up to 36,000 specimens on one slide) and rather diverse (200 species) diatom assemblage was found. *Paralia sulcata*, *Detonula confervacea*, and *T. nitzschiodes* dominate. The age-determinative species *A. divisus* and *A. ochotoensis* are noted. The proportion of pelagic-planktonic species is appreciable. The assemblage is neratic but more deep-water than in section 755 and bore-hole 341. The diatom assemblage in bore-hole 3 is less abundant (up to 3000 specimens on one slide), but more varied (217 species). *Paraliasulcata*, *D. confervacea*, *Chaetoceros* spores, *R. hebetata f. hiemalis*, *T. nitzschioides*, *N. distans*, and *Nitzschia ovalis* dominate. The presence of *T. nidulus*, *A. divisus*, *A. ochotoensis*, and *R. curvirostris* is characteristic for material of this age. Palynological data indicate the middle Pleistocene sediment age. The two latter assemblages were formed in the same basin, and correlation between sea level oscillations and climatic changes has been registered (Loseva and Durjagina 1989).

The middle Pleistocene assemblages were also found in several other sections in the region. Overall more than 390 species of diatoms and Silicoflagellatae were noted, including more than 320 Quaternary taxa, which considerably exceeds the number of species in early Pleistocene assemblages. Of these 73 % are marine and 27 % are freshwater species. *Paralia sulcata*, *T. nitzschioides*, *N. distans*, *T. antarctica*, *C. holsaticus*, *C. mitra*, *N. ovalis*, *R. hebetata f. hiemalis*, and *D. confervacea* dominate. In all sections *H. obsoletus*, *Bacterosira fragilis*, *Synedra tabulata*, *Cocconeis costata*, *T. oestrupii*, *Porosira glacialis*, and *Chaetoceros armatrus* are present and often abundant. The genera *Cocconeis* (24 species), *Navicula* and *Diploneis* (23), *Nitzschia* (18), and *Thalassiosira* (17) are the most varied. The characteristic species are shown in Plate 2. As in the early Pleistocene assemblages, the age-determinative species include *T. nidulus*, *A. divisus*, *A. ochotoensis*, and *R. curvirostris*. *Thalassiosira angulata*, *T. baltica*, *T. nordenskioeldii*, *Synedra*

kamtschatica, *Rhabdonema arcuatum f. contracta*, *Grammatophora oceanica* var. *macilenta f. nodulosa*, *Navicula pennata*, *N. spuma var. minor*, *Diploneis smithii* var. *rhombica*, *Cocconeis californica*, *C. decipiens*, *C. infirmata*, *C. scutellum* var. *stauroneiformis*, *Achnanthes taeniata*, *Rhoicosphenia curvata*, *Nitzschia cylindrus*, and *N. grunowii* are also common in early and middle Pleistocene assemblages and are absent in younger ones in this region. At the same time middle and upper Pleistocene assemblages share a number of species that are not observed in the early Pleistocene: *Psammodiscus nitidus*, *Opephora marina*, *Dimerogramma minor*, *Lyrella forcipata* var. *densestriata*, *Navicula latissima*, *Cocconeis pseudodiscullus*, *Achnanthes hauckiana*, etc. Moreover, some species common in upper Pleistocene assemblages are more abundant here than in early Pleistocene. These include, *P. glacialis*, *D. confervacea*, *Zygoceros rhombus*, *Chaetoceros holsaticus*, *C. mitra*, *Cymatosira belgica*, *R. hebetata f. hiemalis*, *D. surirella*, *N. distans*, and *N. ovalis*. These features of the composition of diatoms allow determination of the middle Pleistocene assemblages.

Upper Pleistocene Diatom Assemblages

The upper Pleistocene marine diatom assemblages were studied in four locations in the western part of the region. The assemblage from section 30a (Pioza River basin) is rather abundant (up to 16,000 specimens occurring on one slide). *Paralia sulcata*, *Podosira stelliger*, *C. belgica*, *R. rhombica*, *D. surirella*, and *N. distans* dominate. The assemblage is littoral; the proportion of planktonic diatoms is insignificant. There are species that are not found in modern northern seas, including *Glyphodesmis distans*, *Opephora schwartzii*, *Diploneis chersonensis*, and *D. crabro*. They are indicative of more warm water conditions than in the Recent White Sea.

In the Pas'va section (the Vaga River middle current), the diatom assemblage is varied (213 species) and very abundant (up to 63,000 specimens on one slide). *Cyclotella caspia*, *D. confervacea*, *Chaetoceros mitra*, *T. nitzschioides*, *Nitzschia navicularis*, *N. ovalis*, and other species dominate. On the whole, the assemblage is littoral-neritic, more indicative of warmer conditions than recent assemblages.

Diatoms from sections 3 and 4 (also the Vaga River basin) are considered as one assemblage. They are less abundant than in Pas'va (up to 6,000 specimens on one slide), but more varied (273 species and varieties). *Nitzschia navicularis*, *P. sulcata*, *D. confervacea*, *C. belgica*, *D. surirella*, *Coscinodiscus granulosus*, *Chaetoceros* spores, and others dominate. The assemblage is littoral and suggest a warm-water environment.

Overall, upper Pleistocene marine diatom assemblages contain more than 360 Quaternary species and varieties and 11 ancient, redeposited ones (Table 1). Freshwater species account for about 27 % of Quaternary species. The assemblages are littoral, warm-loving, and tend toward fresh water. *Hyalodiscus obsoletus*, *Z. rhombus*, *C. belgica*, and *D. surirella* dominate. The characteristic species are shown in Plate 3. The age-determinative species, mentioned above, are absent.

Discussion

It is necessary to answer two main questions: 1) the conditions of formation, and 2) the ages of the sediments investigated. The marine diatom assemblages considered above have similarities as well as differences. All assemblages were formed in littoral or neritic conditions, in waters of different salinity and temperature. The early Pleistocene assemblage in the region is the most deep-water (23 % planktonic species), the most marine (45 % polyhalobous), and the most cold-water (21 % northern, 34 % warm-water species). The upper Pleistocene assemblage is the most diverse and abundant, and it contains the

TABLE 1. The diatom composition in the type sections. Abbreviaions: m—marine; f—freshwater; a.r.—ancient redeposited; *—together with Silicoflagellatae.

Age	Base sections	Q species			a.r.*	Total*
		m	f	sum		
Q_3	Piosa, 30a	96	20	116	9	125
	Pas'va	174	39	213	–	213
	Vaga, 3,4	206	64	270	3	273
	Sum in Q	265	97	362	11	373
Q_2	341	154	50	204	39	244
	755	102	13	115	34	149
	3	150	46	196	21	217
	502	167*	21	188*	12	200
	Others	70*	22	92*	54	146
	Sum in Q	240*	88	328*	71	399
Q_1	SDK-80	79	24	103	29	132
	74	84	27	111	47	158
	1-JA	101	32	133	34	167
	53	46	6	52	21	73
	Sum in Q	150	53	203	59	262
	Total in Q	330*	150*	480*	80	560

most shallow-water (14 % planktonic), the most warm-water (15 % northern and 42 % warm-water species), and the least marine (40 % polyhalobous) taxa. The middle Pleistocene assemblage has intermediate characteristics.

The duration of the Quaternary, according to the stratigraphical schemes used in the USSR, is from 0–0.8 m.y., corresponding to the Brunhes magnetic epoch, and its subdivisions have the following duration: Holocene, 0–10 Kyr; upper Pleistocene, 10–110 Kyr; middle Pleistocene, 110–380 Kyr; and early Pleistocene, 380–800 Kyr (Krasnov and Zarrina 1987).

It is quite difficult to correlate the diatom assemblages of northeastern Europe with Cenozoic diatom zones of other regions, because the zonation in other regions has been worked out for deep-water sediments while the assemblages in our region are rather shallow-water, and a number of the pelagic-planktonic species, typical of ocean sediments, are absent here. In the Norwegian Sea of the North Atlantic, within the Pleistocene (the duration of which is 1.8 m.y. according to the stratigraphical schemes of the Atlantic), only one diatom zone (the *T. oestrupii* zone) is distinguished (Schrader and Fenner 1976). Given that in northeastern Europe *T. oestrupii* is found in all diatom assemblages of different ages, all assemblages can be related to this one diatom zone, *T. oestrupii*.

The subdivision of this zone into shorter sections is possible by taking into account the peculiarities of the diatom assemblages. The most distinctive boundary, suggested by the diatoms, is observed between the middle and upper Pleistocene. The age-determinative species *T. nidulus*, *A. divisus*, *A. ochotoensis*, *R. curvirostris*, and some others are found only in lower and middle Pleistocene sediments. They had become locally extinct before the moskovskoje glaciation, i.e., about 125 Kyr. The early and middle Pleistocene diatom assemblages have many common features, but in the latter's composition there is a number

of species that are more characteristic of upper Pleistocene assemblages (*P. nitidus*, *O. marina*, *D. minor*, and others). Some species play a more significant role here than in the early Pleistocene assemblages (*P. glacialis*, *D. confervacea*, *C. belgica*, *Z. rhombus*, *R. hebetata f. hiemalis*, *D. surirella*, and others). In upper Pleistocene assemblages the age-determinative diatoms are absent, while many species reach considerable abundance for the first time.

In summary, all Pleistocene marine diatom assemblages in northeastern Europe belong to one diatom zone, the *Thalassiosira oestrupii* zone, and may be divided into three age groups, based on the diatom composition of the assemblages.

Acknowledgements

I am grateful to all my colleagues from the Institute of Geology and other departments, who helped me and made useful remarks.

Literature Cited

GUSLITZER, B. I., E. I. LOSEVA, ET AL. 1986. The Timan-Pechora-Vychegda region (Scheme II). Decisions of 2 interdepartmental stratigraphic meeting about Quaternary of East Europe Platform. Leningrad: 25–38.

KRASNOV, I. I. AND E. P. ZARRINA. 1987. The interregional stratigraphic scheme of Quaternary sediments of ezast-European platform and its comparison with other geochronical scales. Pp. 19–23 *in* Cenozoic sediments and structural geomorphology of the U. S. S. R. XII Congress INQUA). Leningrad.

LOSEVA, E. I. 1992. Atlas of marine Pleistocene diatoms of northeastern European part of the U. S. S. R. L., "Nauka." Leningrad.

LOSEVA, E.I. AND D.A. DURJAGINA. 1989 The subdivision of Quaternary sediments in northwest Pritimanje. Sci. works of the Geological Institute of Komi Sci. Center., 73:62–74.

SCHRADER, H.-J. AND J. FENNER. 1976. Norwegian sea Cenozoic diatom stratigraphy and taxonomy. Init. Repts. Deep Sea Drilling Project 38:921–1099.

Explanation of Plates

Plate 1, Figures 1–17

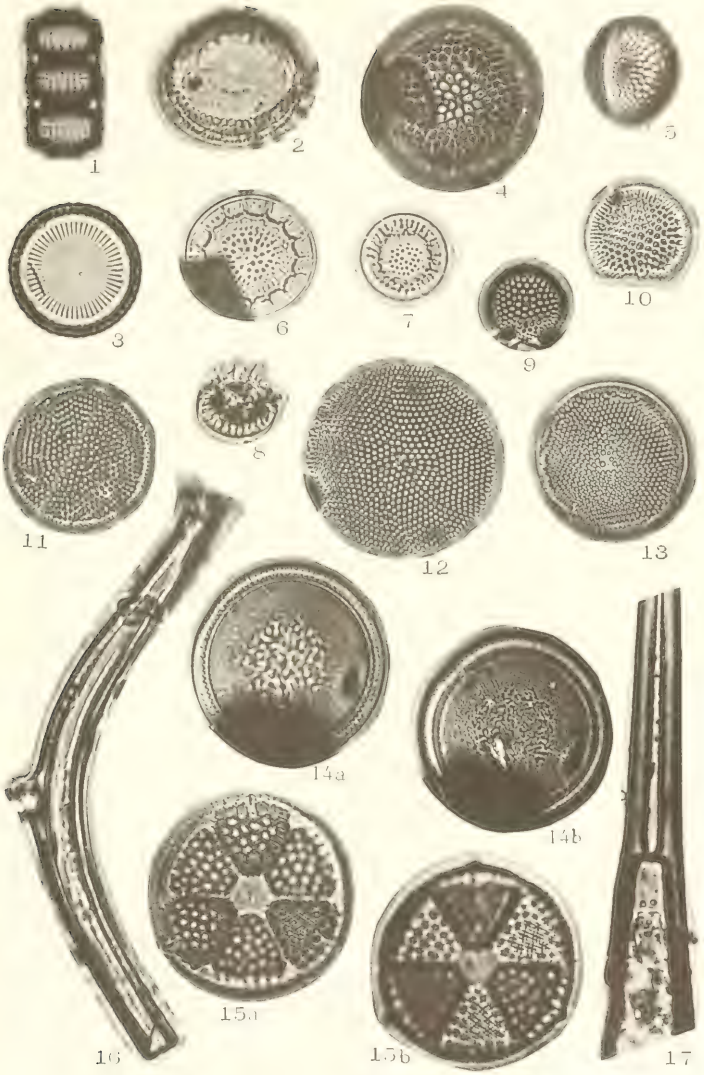
FIGURES 1–17. Some characteristic diatoms from kolvinskaja suite (Early Pleistocene; Q_1). All figures x 1000. FIGURES 1–3. Paralia sulcata var. *sulcata*. FIGURES 4, 5. *Thalassiosira antarctica*, spores. FIGURES 6–8. *T. nidulus*. FIGURES 9, 10. *T. oestrupii*. FIGURE 11. *Actinocyclus divisus*? FIGURE 12. *A. curvatulus*. FIGURE 13. *A. ochotoensis*. FIGURES 14a, b. *Hyalodiscus obsoletus*. FIGURES 15a, b. *Actinoptychus senarius*. FIGURE 16. *Rhizosolenia curvirostris*. FIGURE 17. *R. hebetata* f. *hiemalis* (Figures 1–5, 8–10, 12–15, 17 from 74 bore-hole; Figures 6, 7, 16 from 1-Ja bore-hole; Figure 11 from SDK-80).

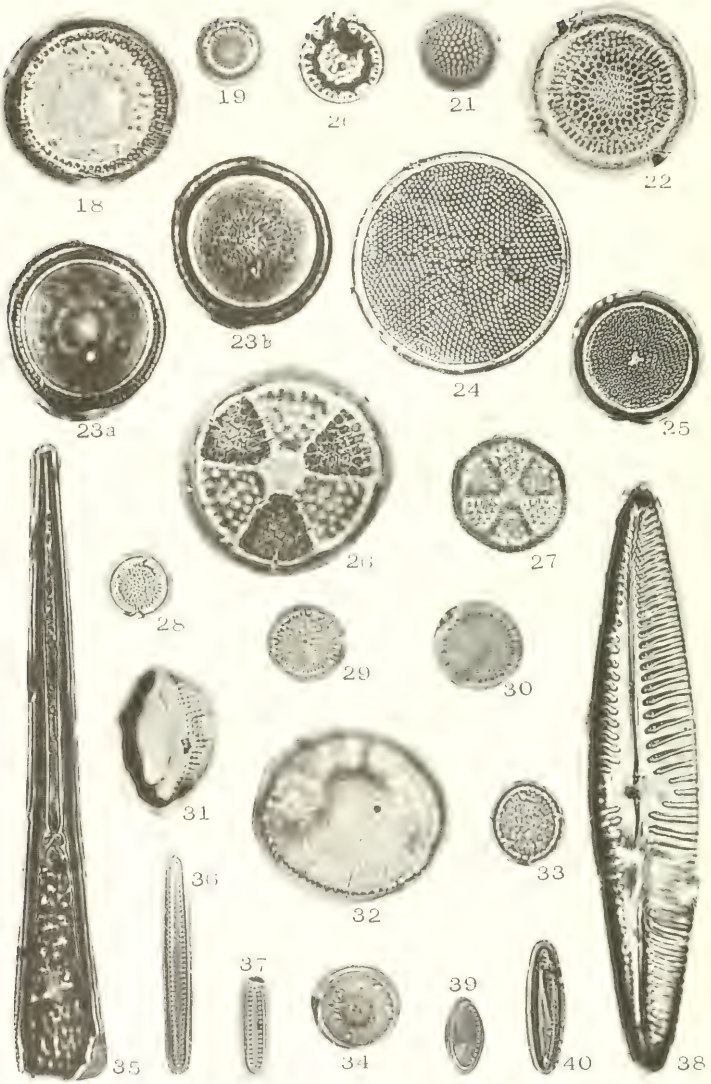
Plate 2, Figures 18–40

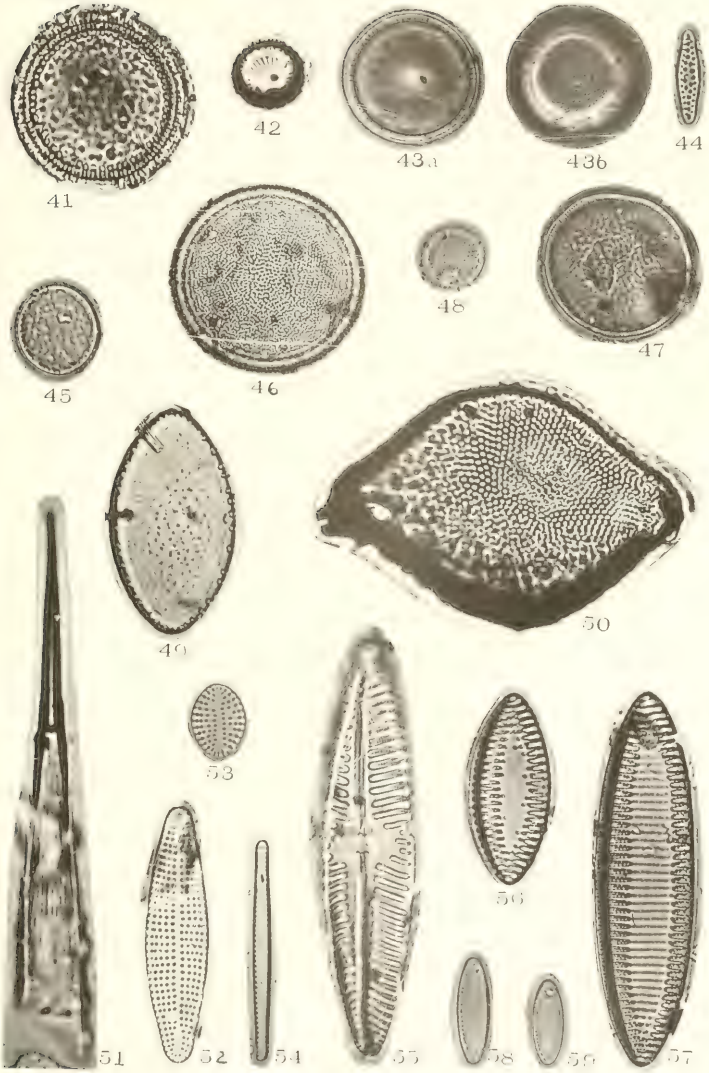
FIGURES 18–40. Some characteristic diatoms from shklovskij horizon (Middle Pleistocene; Q_2). All figures x 1000. FIGURES 18, 19. *Paralia sulcata*. FIGURE 20. *Thalassiosira nidulus*. FIGURE 21. *T. oestrupii*. FIGURE 22. *T. antarctica*, spore. FIGURES 23a, b. *Hyalodiscus obsoletus*. FIGURE 24. *Actinocyclus curvatulus*. FIGURE 25. *A. ochotoensis*. FIGURES 26, 27. *Actinoptychus senarius*. FIGURES 28–30. *Detonula confervacea*. FIGURES 31, 32. *Chaetoceros mitra*. FIGURE 33. *C. holsaticus*. FIGURE 34. *Bacterosira fragilis*. FIGURE 35. *Rhizosolenia hebetata* f. *hiemalis*. FIGURES 36, 37. *Thalassionema nitzschioides*. FIGURE 38. *Navicula distans*. FIGURES 39, 40. *Nitzschia ovalis* (Figures 18–20, 26, 31, 37 from 3 bore-hole; Figures 21, 27, 34 from 755 section; Figures 22–25, 29, 30, 32, 33, 35, 38, 40 from 502 bore-hole; Figures 28,36,39 are from 341 bore-hole).

Plate 3, Figures 41–59

FIGURES 41–59. Some characteristic diatoms from mikulinskij horizon (Upper Pleistocene; Q_3). All figures × 1000. FIGURES 41, 42. *Paralia sulcata*. FIGURES 43a, b. *Hyalodiscus obsoletus*. FIGURE 44. *Cymatosira belgica*. FIGURE 45. *Chaetoceros* holsaticus. FIGURE 46. *Porosira glacialis*. FIGURE 47. *Coscinodiscus granulosus*. FIGURE 48. *Detonula confervacea*. FIGURE 49. *Chaetoceros mitra*. FIGURE 50. *Zygoceros rhombus*. FIGURE 51. *Rhizosolenia heletata* f. *hiemalis*. FIGURES 52, 53. *Delphineis surirella*. FIGURE 54. *Thalassionema nitzschioides*. FIGURE 55. *Navicula distans*. FIGURES 56, 57. *Nitzschia navicularis*. FIGURES 58, 59. *N. ovalis* (Figures 41, 50 from Piosa; Figures 42, 45, 47, 49, 54, 57, 58 from Pas'va; Figures 43, 44, 46, 48, 51–53, 55, 56, 59 from Vaga).


1
2
3
4
5
6
7
8
9
10
11
12
13
14a
14b
15a
15b
16
17


18
19
20
21
22
23a
23b
24
25
26
27
28
29
30
31
32
33
34
35
36
37
39
40
38


41
42
43a
43b
44
45
46
48
47
49
50
51
52
53
54
55
56
58
59
57

Shore Displacement in the Stockholm Area, Sweden, During the Early Holocene as Recorded From Diatom and Magnetic Analysis— A Preliminary Report

by

J. Risberg

Stockholm University, Department of Quaternary Research,
Odengatan 63, S-113 22 Stockholm, Sweden

and

P. Sandgren

Lund University, Department of Quaternary Geology,
Tornavägen 13, S-223 63 Lund, Sweden

with 8 figures

Abstract: The sediment strata in three basins close to Stockholm, Sweden, have been investigated with respect to diatom and magnetic stratigraphy. Results are presented as total diatom diagrams and diagrams of magnetic susceptibility, SIRM, HIRM, and S-ratio, respectively.

During the early Litorina stage there was a transgression starting after 8000 ^{14}C years B. P., having its transgressional maximum around 7000 B. P. From one site, the "Northern" fen in Kyrktorp (49 m a.s.l.), there is evidence of a minor transgression with its maximum preliminary dated to about 6100 ^{14}C years B. P. This transgression seems not to have affected the composition of the diatom flora within the other two basins, Lake Ädran and the Tullinge fen, since these are situated at lower altitudes than the "Northern" fen (+45 and +46 m a.s.l., respectively).

Introduction

From the Stockholm area and the Södertörn peninsula, south of Stockholm (Fig. 1), several shore displacement curves have been published since the end of the 1920s. The oldest of these curves (Granlund 1928) shows no sea level fluctuations during the last 6000 years, but only a steady regression. In later published papers evidence of four transgressional

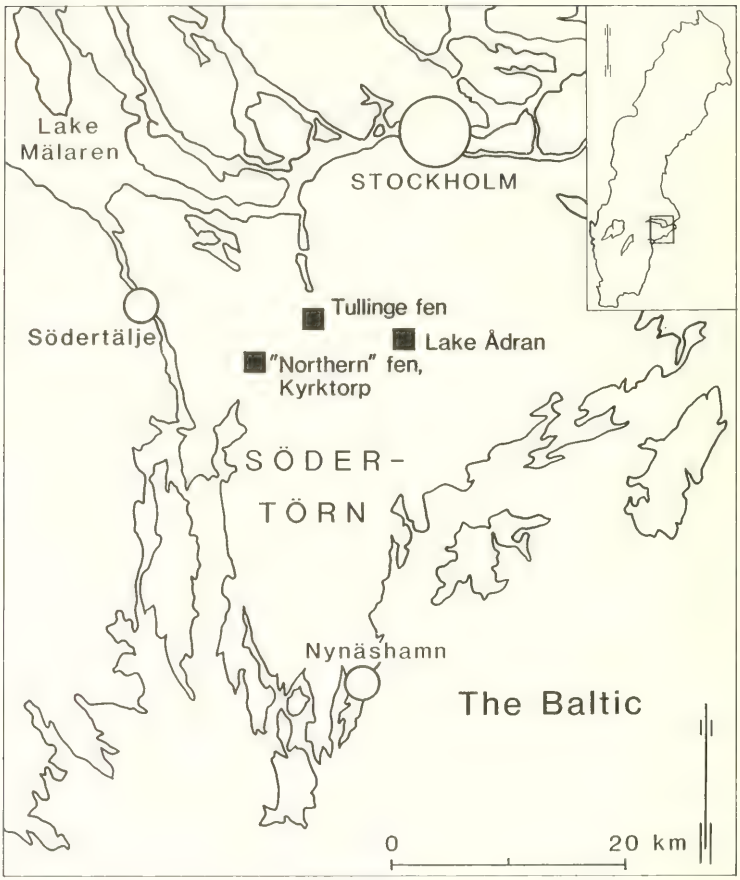


FIGURE 1. Location of sites investigated.

phases during the early Litorina stage has been recorded from archaeological and geological records (Florin 1944; Miller and Robertsson 1981; Miller *in* Brunnberg et al. 1985). In the tentative shore displacement curve constructed by Miller (*in* Brunnberg et al. 1985) two distinct transgressive phases (L1 and L2) during the early Litorina (7500–6000 ^{14}C years B.P.) are reported. The amplitude of L1 was estimated to c. 5 m, and the highest level was estimated to around + 50 m. The amplitude of L2 was estimated to c. 4 m, and the highest sea level occurring during L2 was estimated to around + 54 m, corresponding to the Litorina limit (LL). In the Södertälje area, about 40 km southwest of Stockholm (Fig. 1), the LL has been determined to + 56 m (Florin 1957).

From Lake Ådran on the Södertörn peninsula Sandgren and Risberg (1990, Fig. 7) presented a shore displacement curve. From 9900 B.P. to 6000 B.P. the LL limit was estimated to + 59 m. Only one transgression was identified.

The aim of this paper is to present additional information of early Litorina sea level changes based on two more sites situated on the Södertörn peninsula; the Tullinge fen and the "Northern" fen in Kyrktorp. Compared to the threshold of Lake Ådran at + 45.0 m (Annerberg and Risberg 1984), the threshold for the Tullinge fen has been levelled to + 46.0 m, and the one at Kyrktorp to + 49.1 m. The levelling methods used are described in Risberg (1989a).

Lake Ådran is situated in an area dominated by bedrock outcrops partly covered by thin till layers. Three major streams enter the lake. The Tullinge fen and the "Northern" fen in Kyrktorp are situated in close proximity to glaciofluvial deposits. No streams enter these lakes; they are affected only by surface runoff and unknown, if any, groundwater inflows. The geographical positions of the three sites are shown in Fig. 1.

Results of pollen analysis and grain size distribution of the Lake Ådran sediments have been published earlier (Risberg and Karlsson 1989; Risberg 1989b). Preliminary results of diatom analyses, presented as a succession diagram, have been reported by Risberg (1988). Magnetic analyses and core correlations of the Lake Ådran sediments have been published by Sandgren and Risberg (1990) and Sandgren et al. (1990).

In this paper diatom analysis and magnetic analyses from the three sites (two fens and the earlier presented results from Lake Ådran) is presented and discussed. A preliminary shore displacement curve showing water level changes during the Holocene is also shown.

Materials and Methods

Sediments were sampled with a 1 m long Russian peat corer with an inner diameter of 5 cm (Aaby and Digerfeldt 1986). The stratigraphy of each sediment core was determined in the field and is shown in the diatom diagrams (Figs. 2, 4, 6).

Preparation of samples for diatom analyses was carried out according to Battarbee (1986). The diatom floras of Cleve-Euler (1951–1955), Mölder and Tynni (1967–1973), and Tynni (1975–1980) were used as an aid to identification and information of ecology.

Samples for magnetic analyses were continuously taken at 1 cm intervals in the two fen sites and at every 5 cm at Lake Ådran. Samples were dried and weighed before the magnetic analyses were carried out. The magnetic susceptibility was measured on the air-dried samples in a Bartington susceptibility bridge. After saturation in a magnetic field of 0.72 Tesla (T), the Saturation Induced Remanent Magnetisation (SIRM) was measured on a Molspin Spinner Magnetometer. SIRM is largely a measure of the concentration of ferrimagnetic minerals in a sample but, compared to susceptibility, is more strongly affected by the magnetic grain size and by any antiferromagnetic minerals. Also in contrast to susceptibility, SIRM is unaffected by paramagnetic components. The samples then were magnetized in a reversed field of 0.1 T ($IRM_{-0.1T}$) and the magnetization similarly measured. The S-ratio (S), roughly a ratio between antiferromagnetic and ferrimagnetic minerals, was calculated as $S = IRM_{-0.1T}/SIRM$. The High Induced Remanent Magnetisation (HIRM) was calculated as (1-S)SIRM/2. HIRM is a rough measure of the concentration of antiferromagnetic minerals in the sample.

All radiocarbon datings have been carried out by Göran Possnert at The Svedberg Laboratory, Uppsala University, using the tandem accelerator technique. Note that the

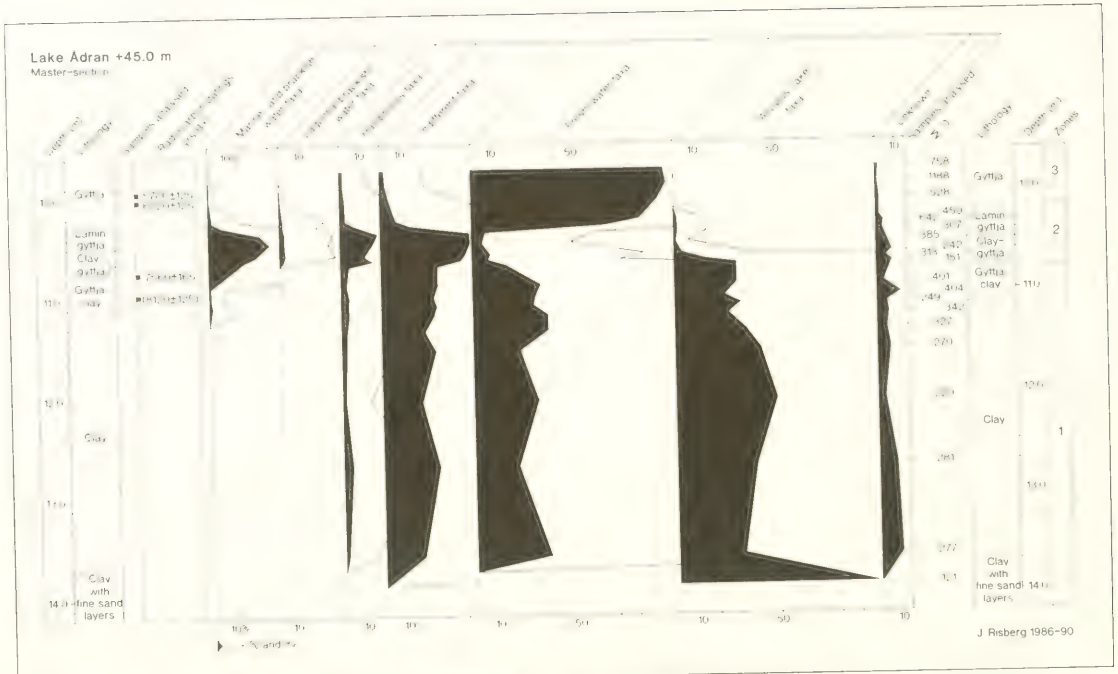


FIGURE 2. Total diatom diagram for Lake Ådran. The radiocarbon date in brackets is from another sediment core but was correlated to this core using magnetic susceptibility (cf. Sandgren et. al 1990).

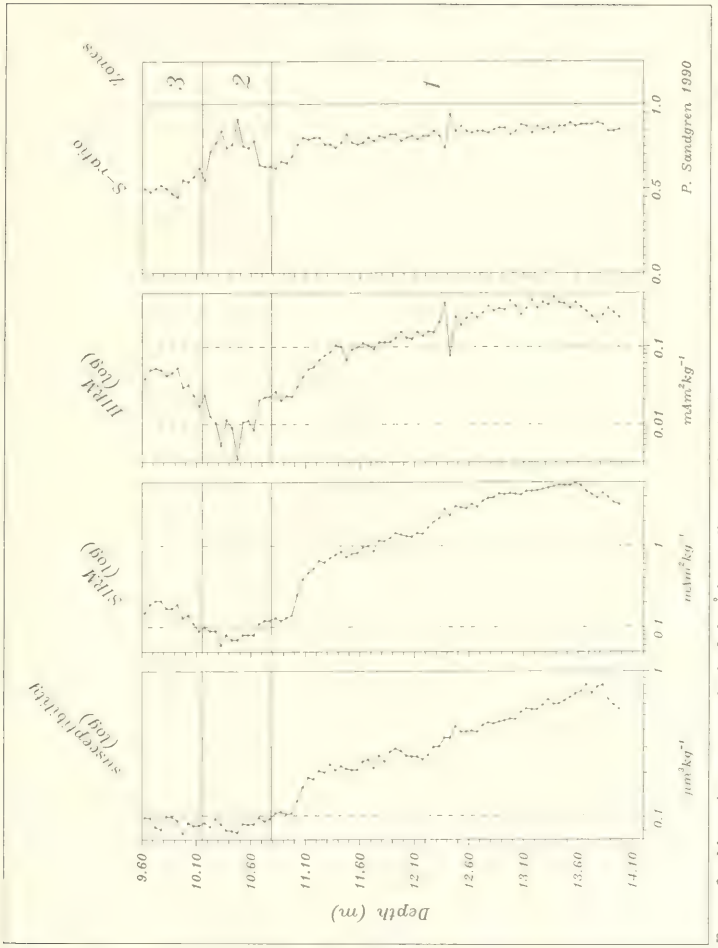


FIGURE 3. Magnetic parameters in the Lake Ådran sediments. Note the logarithmic scale for susceptibility, SIRM, and HIRM.

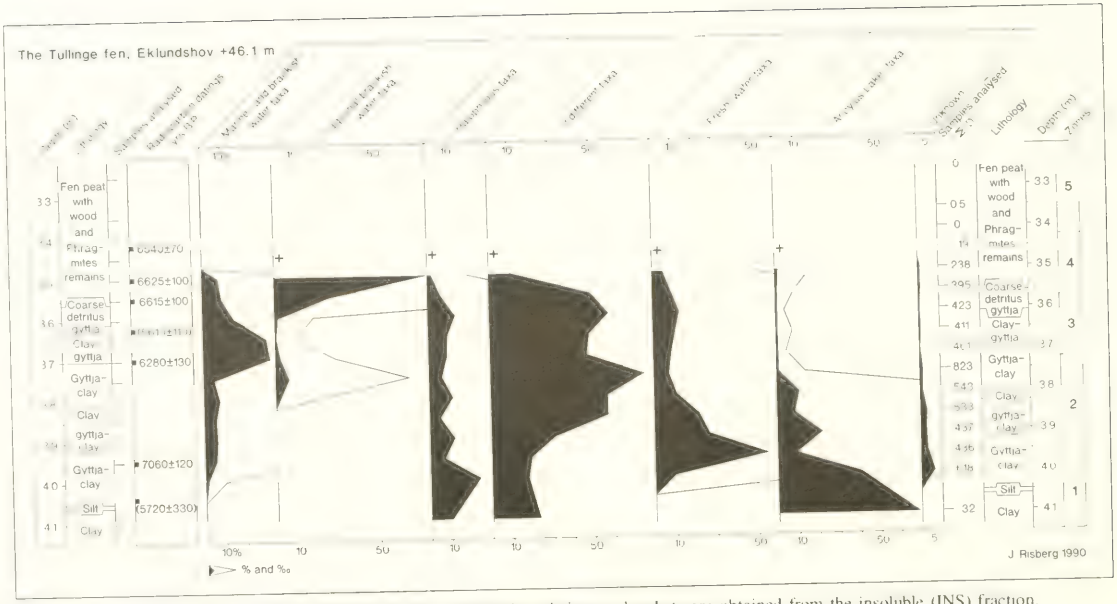


FIGURE 4. Total diatom diagram from the Tullinge fen. Radiocarbon datings in brackets are obtained from the insoluble (INS) fraction.

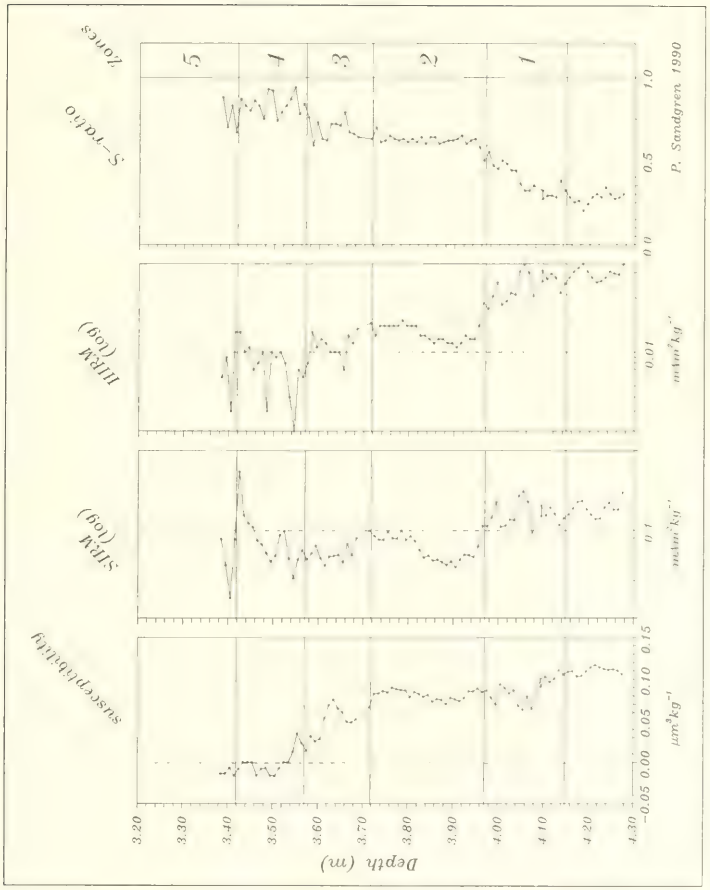


FIGURE 5. Magnetic parameters in the Tullnge fen sediments. Note the logarithmic scale for SIRM and HIRM.

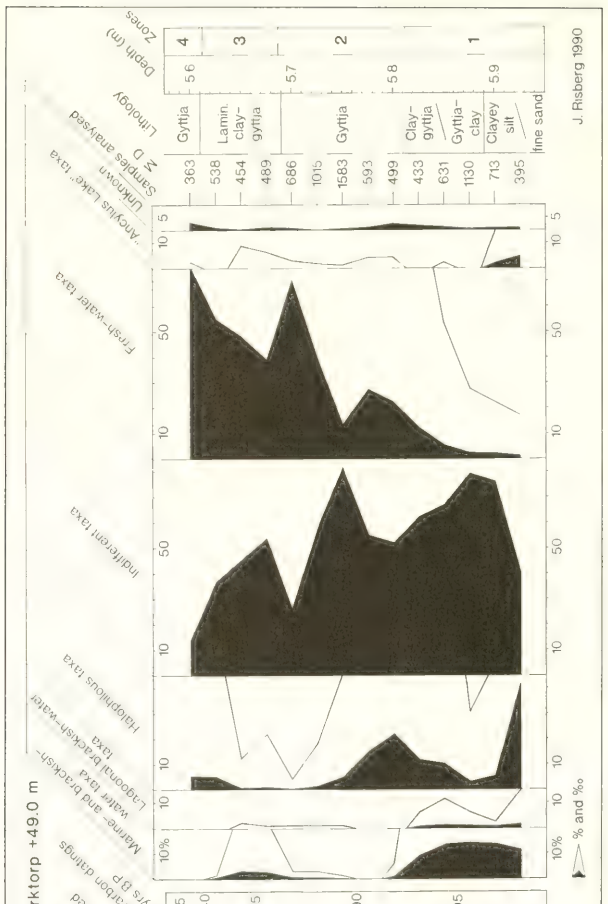


FIGURE 6. Total diatom diagram from the "Northern" fen in Kyrktorp. Radiocarbon dates are preliminary.

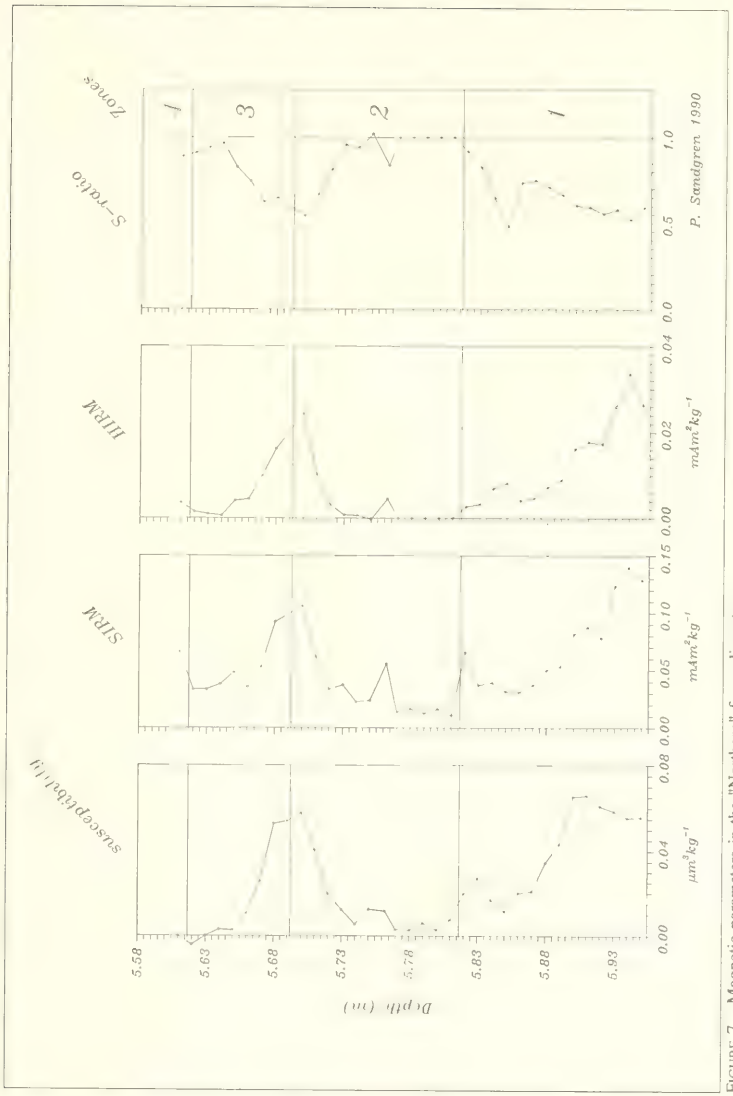


FIGURE 7. Magnetic parameters in the "Northern" fen sediments.

dates for the "Northern" fen in Kyrktorp are preliminary. Therefore no discussion on the chronology is made here.

Results

Results of the diatom analyses are presented as diagrams where the identified taxa have been grouped as follows: marine and brackish water taxa, brackish lagoonal water taxa, halophilus taxa, indifferent taxa, fresh water taxa, "Ancylus Lake" taxa, and unknown taxa. The Ancylus Lake is defined as a freshwater stage of the Baltic Sea between c. 9600 ^{14}C years B.P. (Svensson 1989) and c. 8300 ^{14}C years B.P. (c.f. Eronen 1974; Hyvärinen 1984).

The diatom stratigraphy of Lake Ådran has been divided into three zones (Fig. 2). Zone 1 indicates deposition in the fresh water of the Ancylus Lake. Typical diatom taxa are *Melosira islandica* Müller + ssp. *helvetica* Müller, *Stephanodiscus astraea* (Ehrenberg) Grunow + var. *minutula* (Kützing) Grunow, *Diploneis maulerii (Braun) Cleve, and Gomphocymbella ancyli* (Cleve) Hustedt.

Sedimentation in Zone 2 occurred in a brackish water environment characterized by *Diploneis smithii* (Brébison) Cleve, *Mastogloia braunii* Grunow, *M. smithii* Thwaites, *Nitzschia hungarica* Grunow, *N. obtusa* W. Smith, and resting spores of *Chaetoceros* spp. In Zone 3 the basin has become isolated from the Litorina Sea and a freshwater lake has been established. Typical diatom taxa are *Cyclotella comta* (Ehrenberg) Kützing + var. *radiosa* Grunow, *C. stelligera* Cleve et Grunow, *Melosira italica* (Ehrenberg) Kützing, and *M. distans* (Ehrenberg) Kützing.

The magnetic parameters of Lake Ådran are presented in Figure 3. Zone 1 is characterized by decreasing susceptibility, SIRM and HIRM values. When the first marine-brackish water taxa appear, between 11.2 and 11.0 m, there is a significant drop in all these three parameters, e.g., SIRM decreases from 0.6 to 0.15 mAm^2kg^{-1} and HIRM from 0.06 to 0.015 mAm^2kg^{-1}. In zone 2, corresponding to the highest occurrence of marine–brackish water diatoms, SIRM and HIRM display the lowest values. SIRM values reach a minimum of about 0.07–0.08 mAm^2kg^{-1}; HIRM values reach a minimum of about 0.05 mAm^2kg^{-1}. Along with the disappearance of these taxa in zone 3, SIRM and HIRM again increase. Following Snowball and Thompson (1988) the low concentrations of both ferrimagnetic as well as antiferromagnetic minerals in zone 2, represented by the low SIRM and HIRM values respectively, were attributed to dissolution of magnetic minerals in the saline water (Sandgren and Risberg 1990). The variations in the S-ratio (Sandgren and Risberg 1990, zones A–D, Fig. 3) were attributed to water level changes as a result of the specific topographical conditions in the Lake Ådran area. The high S-ratios (Sandgren and Risberg 1990, zone A and C, Fig. 3) are characterized by a regional type of magnetic minerals with a water level above + 59 m.

The diatom stratigraphy of the Tullinge fen has been divided into five zones (Fig. 4). During zone 1, deposition occurred in the Ancylus Lake as reflected by typical diatom taxa such as *Melosira islandica* + *ssp. helvetica*, *Stephanodiscus astraea* + var. *minutula*, *Navicula tuscula* (Ehrenberg) Grunow, and *Opephora martyi* Héribaud. Zone 2 represents a slightly brackish water environment with the typical diatom taxa *Mastogloia smithii*, *M. braunii* and *Campylodiscus clypeus* Ehrenberg. In zone 3 the sediment was deposited in a brackish water environment as reflected by c. 30 % marine–brackish water taxa, e.g., *Mastogloia braunii*, *M. smithii*, *Nitzschia obtusa* W. Smith and resting spores of *Chaetoceros* ssp. Zone 4 represents a typical *Clypeus* lagoon (cf. Florin 1946) with taxa such as *Campylodiscus clypeus*, *Anomoeoneis sphaerophora* (Kützing) Pfitzer, *Amphora*

mexicana (Cleve) A. Cleve, and *Nitzschia scalaris* W. Smith. In zone 5 diatoms have almost disappeared; only fragments of *Pinnularia* spp. were found.

Similar to Lake Ådran there is a drop in the magnetic susceptibility, SIRM, and HIRM at the transition from zone 1 to zone 2, representing the transition from the Ancylus Lake to a brackish water environment of the Litorina Sea (Fig. 5). In zones 2 and 3 the absolute values of all these three parameters are low and very similar to those in Lake Ådran, ranging between 0.06–0.10 and 0.01–0.02 mAm^2kg^{-1} for SIRM and HIRM respectively. Within this zone of low values it can be noted that the values are slightly higher, between 3.7 and 3.8 m, corresponding to up to 10 % of lagoonal-brackish water taxa as well as slightly different lithological composition. A clear low peak in the susceptibility record is also seen at ca. 3.68 m, corresponding to the highest amount of marine–brackish water taxa. Above that (zone 4) the basin became overgrown and isolated. At this stage very little (magnetic) material could be transported into the basin. This is clearly reflected by the negative susceptibility values seen in the top of the diagram.

The diatom stratigraphy from the "Northern" fen in Kyrktorp is shown in Figure 6. It has been divided into four zones based on the composition of the diatom flora. Zone 1 is dominated by indifferent taxa, e.g., *Epithemia zebra* (Ehrenberg) Kützing, *Fragilaria brevistriata* Grunow, *F. construens* (Ehrenberg) Grunow, and *F. pinnata* Ehrenberg, and marine–and brackish water taxa, e.g., *Amphora lineolata* Ehrenberg, *Diploneis smithii* (Brébison) Cleve, *Mastogloia baltica* Grunow, *Navicula digitoradiata* (Gregory) A. Schmidt, and *Nitzschia obtusa* W. Smith. In zone 2 indifferent taxa together with freshwater taxa dominate almost exclusively. *Melosira distans* (Ehrenberg) Kützing comprises about 55 % of the flora. In zone 3 there is a slight reoccurrence of marine–brackish water taxa, and all taxa identified were recorded in zone 1. In zone 4 there is a dominance of freshwater taxa (comprising ca. 70 % of the flora). Typical genera are *Eunotia* spp. and *Gomphonema* spp., which occur together with *Tabellaria fenestrata* (Lyngbye) Kützing.

Magnetic parameters of the "Northern" fen in Kyrktorp are presented in Figure 7. Again, very low values are recorded in susceptibility, SIRM, and HIRM. Of interest are the extremely low values of susceptibility and SIRM, and HIRM values being almost 0 between ca. 5.75 and 5.80 m, corresponding to the absence of both marine–brackish water taxa and lagoonal brackish water taxa in the lower part of zone 2.

Interpretation

The diatom and magnetic stratigraphies in Lake Ådran are interpreted as a gradual change from deposition in the Ancylus Lake via the *Mastogloia* and Litorina stages to an isolated basin. Contemporary with the influx of brackish water into the basin there was a rise in the sea level. According to Sandgren et al. (1990) and Sandgren and Risberg (1990) the transgression peak occurred around 7200 ^{14}C years B.P. with an amplitude of ca. 6 m. The isolation of Lake Ådran took place at about 5900 ^{14}C years B.P.

Although the stratigraphy of the Tullinge fen does not extend as far back in time as the former site, the general history of this site is interpreted accordingly to Lake Ådran. The significant drop in "Ancylus Lake" taxa and the appearance of marine–brackish water taxa at about 3.95 m indicate a transition from a freshwater to brackish water environment. Correspondingly, at 3.95 m there is a drop in the magnetic parameters, most clearly reflected in the SIRM and HIRM records, to similar low values as seen in the Lake Ådran records during the Litorina stage. There are, however, a pattern of minor variations not seen in the Lake Ådran magnetic records. Possibly the occurrence of lagoonal brackish water taxa between ca. 3.7 and 3.8 m and the slight increase seen in the susceptibility,

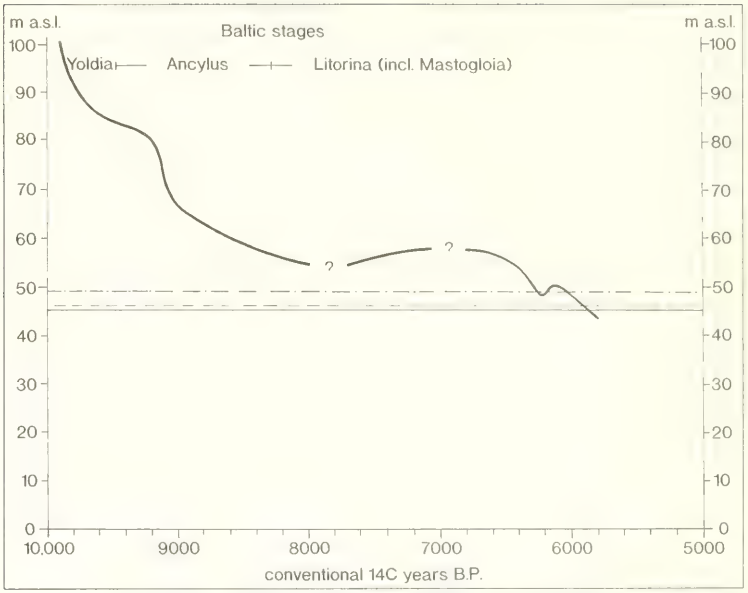


FIGURE 8. Tentative shore displacement curve for Södertörn peninsula based on the three sites included in this paper. The shore displacement curve is based on Sandgren and Risberg (1990, Fig. 7) combined with the evidence of the minor transgression at about 6000 ^{14}C years B.P. in the "Northern" fen in Kyrktorp. Horizontal lines represent, from the bottom, the isolation thresholds of Lake Ådran, the Tullinge fen, and "Northern" fen in Kyrktorp.

SIRM, and HIRM values could be a reflection of the maximum of the regression (Sandgren and Risberg 1990, Fig. 7) before the onset of the Litorina transgression. The maximum of the Litorina transgression is reflected in the diatom diagram by the highest occurrence of marine and brackish water taxa along with a significant drop in magnetic susceptibility and lower SIRM and HIRM values compared to the upper part of zone 2. The final stage, the infilling and overgrowing of the fen, started well before the isolation from the Litorina sea. The gradually lower susceptibility values recorded from c 3.64 m probably are a reflection of this decreasing water level with gradually less minerogenic material settling in the basin.

Compared to the two sites described above, the "Northern" fen in Kyrktorp displays a different pattern both with respect to the diatom and the magnetic stratigraphy. This record is only 35 cm long and it most probably represents an even shorter time period than the Tullinge fen. Zone 1 is interpreted as representing the later parts of the major Litorina transgression. The magnetic parameters of this zone have low values, comparable to the low values of the Litorina stage recorded in the two previously described sites. The slightly higher values seen in the bottom of the records most probably are a reflection of coarser magnetic grains in the clayey silt/fine sand layer in the bottom of the core. The basin became isolated at the beginning of Zone 2, i.e., c. 6800 ^{14}C years B.P. (preliminary

date). This isolation is reflected in the diatom diagram by the absence of marine and brackish water taxa as well as lagoonal brackish water taxa. In addition to this, all magnetic parameters display very low values between 5.81 and 5.75 m, indicating that no deposition of magnetic particles took place as a result of the isolation in combination with a very low water level and no streams entering the small basin. The laminated sequence, represented by zone 3, between 5.69 and 5.61 m with a reappearance of marine–brackish water taxa, is interpreted as reflecting an input of saline water. A preliminary interpretation suggests this occurred between ca. 6200 and 6000 ^{14}C years B.P., indicating a minor transgressional phase. The heavy salt water was sinking to the bottom of the basin causing possibilities for water circulation to decrease. The oxygen within the heavy bottom water was consumed, causing the bottom fauna to disappear. As a result of these undisturbed conditions, a suitable environment for the formation of laminae was established. These assumed water level changes, which occurred after the major Litorina transgression but were not recorded in the two previously described sites, are attributed to the fact that these two sites are situated at lower elevations with the water level well above the isolation threshold.

The preliminary shore displacement during the early Litorina stage, as the combined result of the diatom and magnetic analyses of these three sites on the Södertörn peninsula, is presented in Figure 8.

Conclusion

Based on the diatom and magnetic stratigraphies in these three basins it can be concluded that during the early Litorina phase there was one major transgression. The transgression peaked around 7000 ^{14}C years B.P., with an amplitude of about 6 m. From the highest situated site investigated, there are indications of a minor transgression peaking around 6100 ^{14}C years B.P. This later transgressional phase during the Litorina stage was of a very short duration, with a rise of the water level on the order of 2–3 m.

Acknowledgements

The authors wish to thank the following persons: Urve Miller for critically reading the manuscript, Britta Hörnström for preparing the diatom slides, and Laszlo Madarasz for making the drawings. The investigations was partly financed by the Swedish Natural Science Research Council (NFR).

Literature Cited

Aaby, B. and G. Digerfeldt. 1986. Sampling techniques for lakes and bogs. Pp. 181–194 *in* Handbook of Holocene Palaeoecology and Palaeohydrology, B. Berglund, ed. John Wiley and Sons, Chichester.

Annerberg, L. and J. Risberg. 1984. Ådran och Rudträsket. En undersökning av isoleringskontakterna i två sörmländska sjöar. University of Stockholm, Department of Quaternary Research. Report 3. 88 pp.

Batterbee, R. W. 1986. Diatom analyses. Pp. 527–540 *in* Handbook of Holocene Palaeoecology and Palaeohydrology, B. Berglund, ed. John Wiley and Sons. Chichester.

Brunnberg, L., U. Miller, and J. Risberg. 1985. Project Eastern Svealand: Development of the Holocene landscape. ISKOS 5:85–91.

Cleve-Euler, A. 1951. Die Diatomeen von Schweden und Finnland. I. K. Svenska Vetenskapsakad. Handl. Fjärde Serien 2:1–163.

———. 1952. Die Diatomeen von Schweden und Finnland. V. K. Svenska Vetensakad. Handl. Fjärde Serien 3:1–153.

———. 1953a. Die Diatomeen von Schweden und Finnland. II. K. Svenska Vetensakad. Handl. Fjärde Serien 4:1–158.

———. 1953b. Die Diatomeen von Schweden und Finnland. III. K. Svenska Vetensakad. Handl. Fjärde Serien 4:1–225.

———. 1955. Die Diatomeen von Schweden und Finnland. IV. K. Svenska Ventensakad. Handl. Fjärde Serien 5:1–232.

ERONEN, M. 1974. The history of the Litorina Sea and associated events. Soc. Sci. Fenn. Comm. Phys.-Math. 44:79–195.

FLORIN, M.-B. 1957. Plankton of fresh and brackish waters in the Södertälje area. Acta Phytogeogr. Suecia 37. 144 pp.

FLORIN, S. 1944. Havsstrandens förskjutningar och bebyggelseutveckling i östra mellansverige under senkvartär tid. Geol. Fören. Stockholm Förhandl. 66:551–634.

GRANLUND, E. 1928. Landhöjningen i Stockholmstrakten efter människans invandring. Geol. Fören. Stockholm Förhandl. 50:207– 232.

HYVARINEN, H. 1984. The *Mastogloia* stage in the Baltic Sea history: diatom evidence from southern Finland. Bull. Geol. Soc. Finland 56:99–115.

MILLER, U. AND A.-M. ROBERTSSON. 1981. Current biostratigraphical studies connected with archaeological excavations in the Stockholm region. Pp 167–173 *in* Florilegium Florinis Dedicatum. Striae 14, L.-K. Königsson and K. Paabo, eds.

MOLDER, K. AND R. TYNNI. 1967. Über Finnlands rezente und subfossile Diatomeen. I. C. R. Soc. Geol. Finlande 39:199–217.

———. 1968. Über Finnlands rezente und subfossile Diatomeen. II. Bull. Geol. Soc. Finland 40:151–170.

———. 1969. Über Finnlands rezente und subfossile Diatomeen. III. Bull. Geol. Soc. Finland 41:235–251.

———. 1970. Über Finnlands rezente und subfossile Diatomeen. IV. Bull. Geol. Soc. Finland 42:129–144.

———. 1971. Über Finnlands rezente und subfossile Diatomeen. V. Bull. Geol. Soc. Finland 43:203–220.

———. 1972. Über Finnlands rezente und subfossile Diatomeen. VI. Bull. Geol. Soc. Finland 44:141–149.

———. 1973. Über Finnlands rezente und subfossile Diatomeen. VII. Bull. Geol. Soc. Finland 45:155–179.

RISBERG, J. 1988. The diatom stratigraphy of Lake Ådran basin, Södertörn, central eastern Svealand, Sweden. A preliminary report. Pp. 69–76 *in* Proceedings of Nordic Diatomist Meeting Stockholm 1987, U. Miller and A.-M. Robertsson, eds. University of Stockholm, Department of Quaternary Research, Report 12.

———. 1989a. Stratigraphical methods applied to shore displacement studies. Council of Europe, PACT 24:181–187.

———. 1989b. Grain size distribution of sediment: a comparison between pipette and sedigraph analysis. Geol. Fören. Stockholm Förhandl. 111:247–250.

RISBERG, J. AND S. KARLSSON. 1989. The pollen stratigraphy in a sediment core from Lake Ådran, Södertörn, central eastern Svealand, Sweden. University of Stockholm, Department of Quaternary research, Report 14. 30 pp.

SANDGREN, P. AND J. RISBERG. 1990. Magnetic mineralogy of the sediments in Lake Ådran, eastern Sweden, and an interpretation of early Holocene water level changes. Boreas 19:57–68.

SANDGREN, P., J. RISBERG, AND R. THOMPSON. 1990. Magnetic susceptibility in sediment records of Lake Ådran, eastern Sweden: correlation among cores and interpretation. J. Paleolimnol. 3:129–141.

SNOWBALL, I. AND R. THOMPSON. 1988. The occurrence of Greigite in sediments in Loch Lomond. J. Quat. Sci. 3: 121–125.

SVENSSON, N.-O. 1989. Late Weichselian and early Holocene shore displacment in the central Baltic, based on stratigraphical and morphological records from eastern Småland and Gotland, Sweden. Lundqua Thesis 25, Lund. 195 pp.

TYNNI, R. 1975. Über Finnlands rezente und subfossile Diatomeen. VIII. Geol. Surv. Finland Bull. 274:1–55.

———. 1976. Über Finnlands rezente und subfossile Diatomeen. IX. Geol Surv. Finland Bull. 284:1–37.

———. 1978. Über Finnlands rezente und subfossile Diatomeen. X. Geol Surv. Finland Bull. 296:1–55.

———. 1980. Über Finnlands rezente und subfossile Diatomeen. XI. Geol Surv. Finland Bull. 312:1–93.

Diatoms and Sediment of a Modern Glacial Fjord Environment, Western Spitsbergen

by

Kerstin M. Williams

Institute for Arctic and Alpine Research,
University of Colorado, Boulder, Colorado 80309

and

Steven L. Forman

Byrd Polar Research Center and Department of Geological Sciences
Ohio State University, Columbus, Ohio 43210-1308

with 4 figures and 2 tables

Abstract: Diatom thanatocoenoses and sediment were investigated, both in close proximity to an actively calving tidewater glacier and in the raised marine record. Diatom concentrations in the sediment were consistently low at distances of 30 m from the front of the glacier (260,000–1,200,000 frustules/g dry weight). Continuous changes in diatom composition from 100 % benthic diatoms to 50 % benthic diatoms and 50 % pelagic diatoms can be observed in the transect from the glacier snout to the mouth of the fjord. Diatom frustules were absent from the raised marine deposits, probably a result of a combination of mechanical abrasion during dewatering, disturbance of the sediment, and dissolution in the dolomite rich, high pH sedimentary environment. Sediment particle size was generally uniform (little variation between samples) with silts and clays dominating, except in the location closest (10 m) to the calving glacier front, where coarser fractions were present.

Introduction

An understanding of the influence of glacial marine and near shore environments on the diatom flora is important if this group is to be used as an aid in interpretation and reconstruction of paleoenvironments. The ice-proximal zone of glaciers might be assumed to be an inhospitable environment for phytoplankton communities because of the often very high water turbulence and extreme turbidity of melt water issuing from the glacier terminus. However, little is known about the viability of diatoms in modern high-arctic, ice-proximal marine environments. Zeller et al. (in press) have shown that glacial ice (both land-based and icebergs) contains sufficient nitrogen and phosphate to cause increased plant productivity at ice margins. The nitrogen source is considered to be cosmogenic, deposited both as dry fallout and incorporated in precipitation. Nitrate accumu-

lates on the ice surface during the winter months to be released during spring and summer thaw. Phosphorus is released from the fine grained rock debris incorporated in the glacial ice and dumped in the vicinity of the glacial terminus. Diatom productivity in proximity of icebergs is often high and most likely the result of release of nutrient-laden meltwater (e.g., Parker et al. 1978). Martin et al. (1990) hypothesized that increased iron availability will increase phytoplankton productivity. Several species of iron will probably be released in a glacial tide-water environment, both from eolian dust accumulation on the glacier surface and from englacially transported material, thus enhancing phytoplankton production. Upwelling provides the mechanism for nutrient distribution in close proximity (within 500 m) of a tide-water glacier margin (Horne 1985).

Diatom assemblages are sensitive to pH, water temperature, dissolved nutrients and oxygen, as well as availability of trace metals. In addition, the length of the growing season and duration and thickness of seasonal ice cover, together with the amount of incident light, interact to determine the success and community composition of the diatom assemblages (e.g., Anderson et al. 1986; Charles 1985). If the response of the diatom assemblages to changes in some or all of these environmental variables can be determined, then, by analogy, the assemblages can serve as a tool for paleoenvironmental reconstruction.

Diatoms in glacier-front zones respond to changes in relative location of the glacier snout in a fashion probably more dramatic than formerly realized. Changes in benthic/pelagic diatom ratios seem to occur in Engelskbukta from directly in front of the glacier snout to as far as 3–4 km away. If such changes can be documented in the fossil record (such as in marine cores or raised marine sediments), they can perhaps be used to infer the position of the ice front at a specific time. This paper begins with an overview of the sediment and sedimentation processes. Then we report on changes in diatom thanatocoenoses (diatom frustules in contemporary deposits) with distance from the snout of an actively calving tide-water glacier in Engelskbukta, a small, glacially influenced fjord in western Spitsbergen (Fig. 1). Finally we discuss possible reasons for the absence of diatom frustules in the raised marine record.

Area Description

Engelskbukta is a small, shallow fjord on the west coast of Spitsbergen, the largest Island in the Svalbard Archipelago (Fig. 1). The inner part of the fjord is occupied by the terminus of a tidewater glacier, Comfortless Glacier, which is one of several outlet glaciers in the fjord. Engelskbukta trends northwest-southeast (Fig. 1), and seems to have a deeper middle section (> 50 m), also running northwest southeast. Maximum depths of 93 m have been recorded in the outer reaches of Engleskbukta. However, most of the bay has not been charted and no sill has been noted.

Only limited work has previously been done on sediments and the micro-flora and fauna in the fjords of western Svalbard. Elverhoi et al. (1980, 1983) reported on sedimentology and micropaleontology in Kongsfjorden, ca. 10 km north of Engelskbukta (Fig. 1).

During the summer of 1983 a highly turbid surface flow exited from a meltwater tunnel in the northern terminus of the Comfortless Glacier. The turbid layer spread out on the fjord surface and often showed a sharp line of demarcation with the fjord water. The seaward extent of this layer was influenced by locally variable winds; onshore winds constrained the layer to the inner reaches of the fjord, offshore winds extended the layer to the fjord mouth.

Sea-ice cover probably depends on wind patterns, but seems to last from early winter to June. Due to Engelskbukta's lack of a sill and to its rather exposed location, there is an

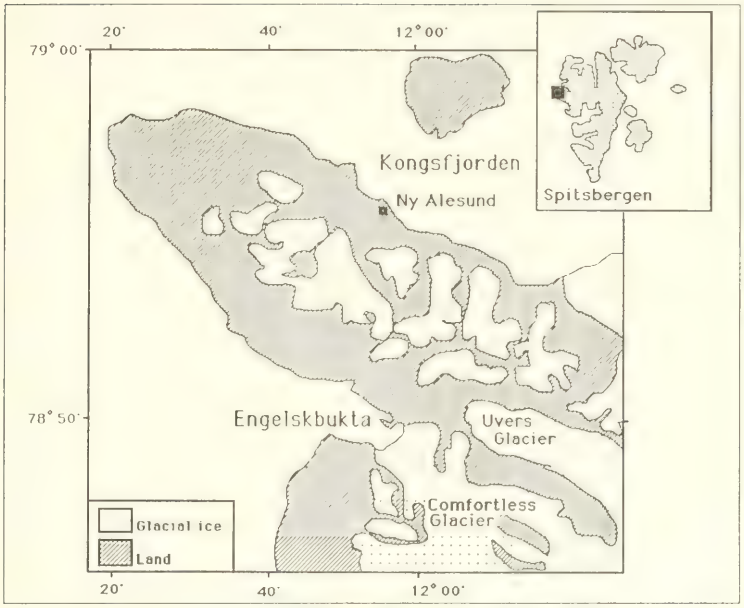


FIGURE 1. Map showing location of study area.

active transit of icebergs and sea-ice in and out of the bay in response to changes in wind direction. The general fjord circulation in Engelskbukta is not known.

Two large valley glaciers, Comfortless Glacier and Uvers Glacier, probably contribute most of the sediment introduced in Engelskbukta. Comfortless Glacier terminates partly in the sea as a calving margin, whereas Uvers Glacier terminates on land. Icebergs are often grounded in the shallow waters adjacent to the Comfortless Glacier's margin, but may also be redistributed in the bay by winds. Icebergs contain a variable amount of debris of different particle sizes that is released by the icebergs overturning and melting in the comparatively warm bay waters. In addition, debris deposited on top of sea-ice by streams or frozen into the ice when it is grounded along shore also contribute a variety of particle sizes to the fjord. Meltwater streams that issue from within and upon this glacier empty into the bay and are a significant sediment source.

The glaciers surrounding the bay end on land as a complex proglacial sandur and moraine sequence (Hambrey 1984). Much of this area is an outwash plain with numerous meltwater streams emptying into Engelskbukta. The sediment discharge from the outwash plain and from Comfortless Glacier enters the fjord as turbid surface overflow that may extend 2 km from the shore. Meltwater streams from the peninsula to the north (Fig. 2) as well as streams from the north side of the bay also contribute sediment to the bay.

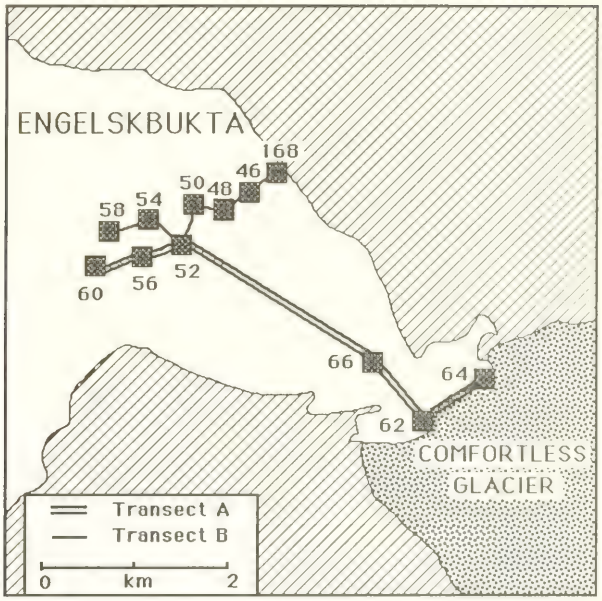


FIGURE 2. Map of Engelsbukta with sample transects A and B. Numbers indicate sample numbers.

Materials and Methods

Twelve surface sediment samples were obtained from the bottom of Engelskbukta with an Ekman grab sampler (Fig. 2). The inherent difficulties and outright dangers of sampling in front of an actively calving glacier dictated sampling density and location. It also proved very difficult to sample in water deeper than 50 m, using a hand-held line and sampler. The samples were from the top 1–2 cm, and were taken along two transects: (A) from the snout of Comfortless Glacier to the outer bay (samples 64, 62, 66, 52, 56, and 60) and (B) from the beach face to a water depth of 48 m (samples 168, 46, 48, 50, 52, 54, and 58 (Fig. 2). Water depth measurements are accurate to 1 m. These transects correspond to those described in Forman (1990).

The 12 samples were analyzed for particle size and diatoms. In all samples, a relatively large percentage of the diatom frustules (> 60 %) was fragmented, and many of the larger frustules were abraded. It should be emphasized that as the samples contained great amounts of glacial flour, identification of diatoms to species level was difficult (because the detrital particles obscured the diagnostic details of the frustules). For diatom analysis a small amount (< 0.5 g) of dry sediment was weighed and boiled in dilute HCl. Marker tablets containing known numbers of *Lycopodium* spores were added to the slurry (Maher 1980). The slurry was then washed with water by repeated centrifuging and decanting.

After the pH of the sediment/water mixture became neutral, slides were made of the sediment and mounted in Hyrax. Diatom frustules were counted according to conventional methods (e.g., Williams 1986). Wherever possible, 300 specimens were counted at 1000 x magnification, together with the number of marker grains encountered. The number of diatoms per gram dry sediment was calculated using the known number of tracer grains added to the sediment. The identifications were made with a VANOX Hoffman Modulation Contrast research microscope. Species with abundance ≥ 2 % are listed in Table 1.

Particle size analyses were made on 100 g of dried sediment. Sand (0.063–2 mm) and gravel (2–16 mm) were separated by wet sieving. Grades finer than 0.063 mm were measured by pipette analysis. Material was unavailable for sediment analysis from stations 48, 54, 58, and 168. Eight Late Quaternary sediment samples were collected and analyzed for diatoms from an emergence sequence on the north side of Engelskbukta. The sedimentology of these samples has been described in Forman (1986).

Results and Discussion

Sediment

Bottom sediments of the fjord are relatively similar in particle size (Fig. 3). They are predominantly a silt-dominated mud with less than 5 % sand and clasts. Particle size distributions are mostly positively skewed, with a dominance of medium silt and clay (Fig. 3). Much of the clay may have flocculated in marine water, forming particles hydrodynamically like silt. Most samples contained 2–4 % organic carbon and had a sulfuric smell upon retrieval, suggesting some bacterial reduction of organic matter.

Only two samples were dominated by particle sizes coarser than silt (Table 2). Sample 64, collected from approximately 10 m off the terminus of Comfortless Glacier, proximal to discharge from an englacial meltwater tunnel, contained 90 % fine sand. Sample 46, collected from 3 m water depth, contained a greater percentage of sand than did deeper samples. The sample was collected from the sublittoral environment, where the wave base had winnowed much of the fine components.

We believe that much of the fjord sediment was transported either as brackish water overflow emanating directly from Comfortless Glacier or through the proglacial fluvial system of Uvers Glacier, and other smaller glaciers within the Engelskbukta watershed. Ice-rafted sand and gravel are minor components of the sediment, significantly diluted by the influx of fines. More variable sedimentology occurred within ca. 30 m of the tidewater glacier front.

Diatoms

General comments: Twelve samples, ranging in water depth from 3–48 m (Table 2) were analyzed for diatoms. Two of these sample sites (64 and 46) are barren of diatoms. Site 64 is located in front of the glacier snout (ca. 10 m distant) and directly outside an englacial meltwater tunnel. Site 46 is located in 3 m of water within the tidal swash zone, immediately off a glacial sandur. Both sample sites were characterized by greater percentage of sand than the other samples, probably as result of winnowing, as mentioned above.

Also, the extreme quantities of sediment being deposited in those environments could inhibit diatom growth, dilute any traces of diatom frustules or destroy them after postmortem deposition. Such destruction probably occurs by mechanical abrasion from the shifting sediment in those highly dynamical environments (Beyens and Denys 1982), or perhaps by dissolution by fresh water with a pH of 8 or above. The freshwater diatoms washed into the marine environment are almost exclusively either circumneutrals or alkaliphils/alkalibionts, indicating freshwater of high pH.

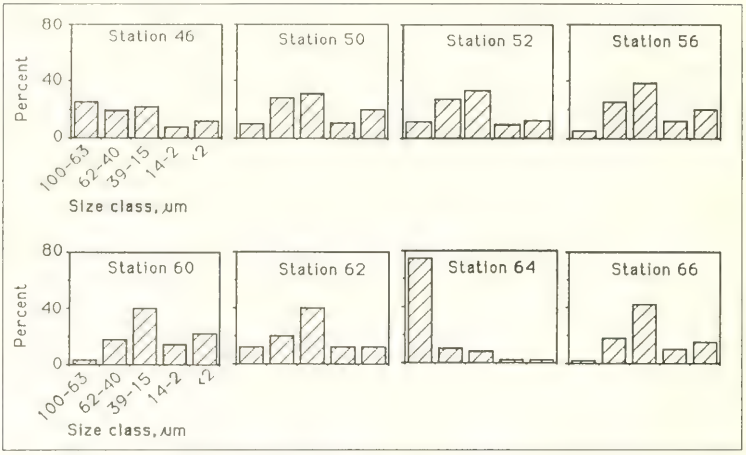


FIGURE 3. Sediment size distribution for each sampling station. X-axis indicates size class, Y-axis indicates %. (Measurements are lacking for stations 48, 54, 58, and 168).

The total number of diatoms preserved in the 10 sediment samples was fairly low (ca. 260,000–1,200,000 diatoms/g dry weight) (Table 2), reflecting dilution by uncommonly high sedimentation rates. Such rates from the inner and central reaches of Kongsfjorden range from 1–100 mm/yr (Elverhoi et al. 1983), and it is likely that the areas under investigation in Engelskbukta have a similar range of sedimentation rates. In contrast, in areas where the sediment consists primarily of diatom frustules, as in many high latitude lakes, total numbers of 60–70 million/g dry weight have been recorded (Clark et al. 1989; Williams 1990a), and 10–12 million/g dry weight from the marine environment along the Baffin Island Shelf is not uncommon (Williams 1990b).

TRANSECT A

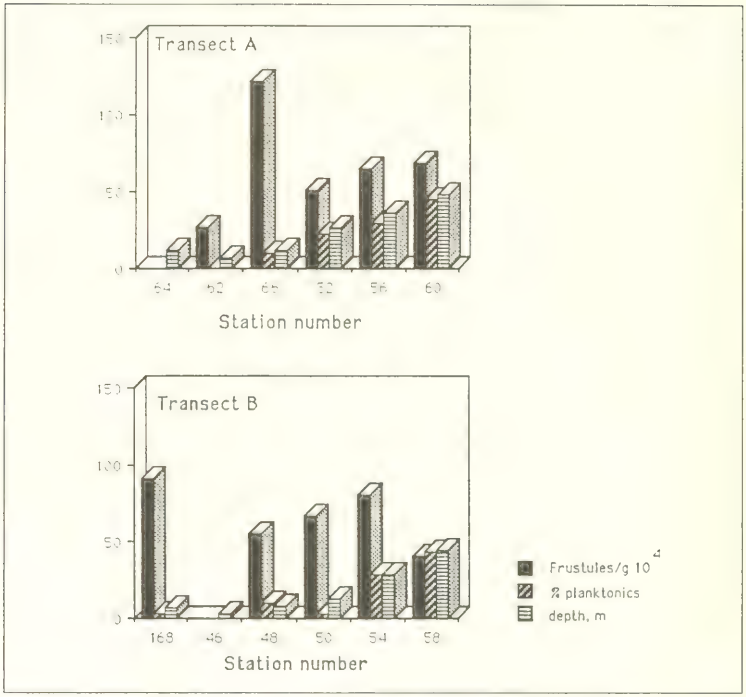
Transect A is composed of sample stations 64, 62, 66, 52, 56, and 60 (from the glacier snout, seawards) (Fig. 2). Numbers of diatoms/g dry weight does not vary much with location, except in station 66 where it reaches a maximum, and in the immediate vicinity of the ice margin (Fig. 2). Sample 64 was collected close to the meltwater stream issuing from the snout of Comfortless Glacier. The sample was barren of diatoms, probably as a result of bottom currents either mechanically destroying the frustules and disturbing the substrate or winnowing the fine size classes. The turbid water may also serve to lower phytoplankton productivity by reducing light penetration (e.g., McDonald et al. 1987). The percent pelagic diatom species increases away from the ice margin (Fig. 4). Sample 62, ca. 30 m off the terminus of Comfortless Glacier, a locality with probably a very high sedimentation rate, has the lowest diatom concentration of all samples where diatoms were present. This sample is dominated mostly by benthic diatoms (*Nitzschia linearis* W. Smith and *Navicula ammophila* Grunow) and *Nitzschia* spp. (Table 1).

Sample 66 has by far the greatest number of diatoms/g dry weight. Apparently the dissolved inorganic nutrients in glacial meltwater are able to support a flourishing diatom flora (Zeller et al. in press; Martin et al. 1990), which develops quickly once the duration of

TABLE 1. Species ≥ 2 % for each station.

Species	SAL	Stations											
		46	48	50	52	54	56	58	60	62	64	66	168
Planktonic diatoms													
Chaetoceros spp. (spores)	M	0	2	0	11	16	11	11	24	0	0	2	0
Nitzschia cylindrus	M	0	2	0	0	0	0	12	0	0	0	0	0
N. grunowii	M	0	0	0	6	4	8	12	4	0	0	0	2
Thalassiosira gravida (spores)	M	0	0	0	0	2	4	0	6	0	0	0	0
T. hyalina	M	0	0	0	2	0	5	0	4	0	0	2	0
Thalassiosira spp.	M	0	0	0	2	5	0	6	3	0	0	2	0
Benthic diatoms													
Achnanthes austriaca v. *helvetica*	F	0	0	0	0	2	2	0	0	0	0	0	0
Achnanthes brevipes	F/M	0	0	0	0	0	0	0	2	0	0	0	0
A. fredskildii	M	0	0	0	0	0	0	0	0	2	0	0	0
A. spp.		0	2	0	6	4	2	2	2	0	0	0	0
Amphipleura spp.		0	0	0	0	0	0	0	0	0	0	4	13
Amphora ovalis	F	0	0	3	2	0	0	0	0	0	0	0	0
Amphora pusio	B	0	0	0	0	0	0	2	0	0	0	0	0
Amphora spp.		0	0	0	0	0	0	0	4	5	0	0	0
Bacillaria paradoxa	B/M	0	0	2	0	0	0	0	0	0	0	0	0
Cocconeis costata	M	0	0	2	0	4	5	6	4	0	0	0	12
Diploneis smithii	M	0	0	0	2	0	0	0	0	0	0	0	0
Entomoneis paludosa	F/M	0	0	0	0	0	0	0	0	2	0	0	0
Fragilaria pinnata	F	0	0	0	2	0	0	0	0	0	0	0	0
Gyrosigma fascicola	B/M	0	0	5	0	2	0	2	0	0	0	0	0
G. acuminatum	F/B	0	18	2	0	0	0	0	0	0	0	19	0
Gyrosigma spp.		0	2	0	0	0	0	2	0	2	0	5	0
Gomphonema gracile	F/B	0	4	3	0	0	2	5	2	0	0	0	0
Gomphonema spp.		0	2	0	0	0	0	0	0	5	0	6	0
Licmophora spp.		0	0	0	0	0	0	2	2	0	0	0	0
Navicula ammophila	M	0	0	29	21	29	27	0	7	19	0	18	13
N. cryptolyra	M	0	2	0	0	0	0	2	0	0	0	0	0
N. directa	M	0	0	0	0	0	0	0	0	0	0	5	0
Navicula spp.		0	4	0	9	2	3	2	0	2	0	3	2
Nitzschia spp.		0	37	5	17	2	0	0	2	12	0	4	9
N. heufleriana	F	0	0	0	0	0	0	0	0	0	0	0	6
N. hybrida	B/M	0	0	19	0	0	0	0	3	0	0	0	0
N. linearis	F	0	0	0	0	0	0	0	0	33	0	6	5
Opephora spp.		0	0	0	0	0	0	6	3	0	0	0	3
Pinnularia spp.		0	0	0	0	2	0	0	0	0	0	0	0
Pleurosigma spp.		0	0	2	0	0	0	0	0	0	0	0	0

F = fresh; M = marine; B = brackish



FIGURES 4A, B. Depth, diatom frustules ($\times 10^4$), and 5 planktonic diatoms for each sampling station along transect A (top) and B (bottom).

daylight and sea-ice conditions permit. However, it is difficult to separate diatom abundance from sedimentation rate in this dynamic environment. The diatom assemblage is dominated by *Gyrosigma acuminatum* (Kütz.) with *Navicula ammophila* as an almost equal component of the flora. *Gyrosigma acuminatum* is considered a freshwater diatom by Tynni (1978) and also by Hustedt (1959), although Hustedt describes two variations of the nominate variety as being brackish. Its presence in such large numbers undoubtedly indicates a governing fresh/brackish meltwater influence at that locality. A few pelagic-diatoms are in evidence, namely *Thalassiosira hyalina* Cleve and *Thalassiosira* spp., as well as spores of *Chaetoceros* spp. Sample 52 is the fourth station on transect A. The diatom assemblage is dominated by benthic diatoms (*Navicula ammophila* and *Nitzschia* spp.) but with an appreciable component of pelagic diatoms (*Chaetoceros* spores). *Nitzschia grunowii* Hasle, the sea ice indicator (Sancetta 1982; Jousé 1962) is also present in this sample.

The next sample along transect A is 56, and it has a steadily increasing pelagic diatom component, composed of *Chaetoceros* spores, *Nitzschia grunowii*, and *T. gravida* (spores). The last sample in this transect, 60, is characterized by an increasing component of marine

Table 2. Depth, frustules/g dry weight, % planktonics and sediment size classes for each station.

	Station	Water depth, m	Frustules / g dry (10^4)	% Planktonics	Sediment Size Class, µm				
					100-63	62-40	39-15	14-2	< 2
transect A	64	12	0	0	75	10	8	2	2
	62	7	26	0	12	20	40	12	12
	66	12	122	10	2	18	42	10	15
	52	26	51	23	12	29	35	10	13
	56	36	65	29	5	5	38	12	20
	60	48	69	45	3	18	40	14	22
transect B	168	7	91	3	–	–	–	–	–
	46	3	0	0	25	19	22	8	12
	48	8	55	10	–	–	–	–	–
	50	13	67	3	10	28	31	11	20
	58	44	40	43	–	–	–	–	–

fluence on the photic zone. As in most other samples, there are freshwater diatoms present—an indication of off-shore transport.

TRANSECT B

A similar trend is evident in the transect from the shore face to deeper water (Fig. 4B). Transect B begins with sample 168, located in ca. 7 m of water about 100 m offshore by a large sandur. The diatom flora is dominated by benthic species (*Navicula ammophila* and *Cocconeis costata* Gregory). *Nitzschia heufleriana* (?) Grunow and *N. linearis* are fresh-water species, probably washed out from the shallow sandur area. *Nitzschia* spp. are represented by 2 %, and the pelagic diatom species (*N. grunowii*) is also represented by 2 %. *Amphipleura* sp. contributes 13 %, but it could not be identified to species and consequently we do not know if it is a marine taxon.

Another barren sample site (sample 46) was located off a large sandur in the swash zone in about 3 m of water. Substrate disturbance and mechanical abrasion as well as winnowing are probably responsible for the lack of diatoms in this case. The following sample, 48, is dominated by benthic diatoms. *Gyrosigma acuminatum* is the most abundant taxon, and it occurs with benthic *Nitzschia* spp.; a few marine pelagic diatoms are also present.

The diatom assemblage in sample 50, the third station of transect B, is dominated almost entirely by benthic diatoms, with *Navicula ammophila* as the most abundant taxon, followed by *Nitzschia hybrida* (?) Grunow. *Amphora ovalis* Kütz. together with *Gyrosigma fascicola* (Ehr.) Griff. & Henfr. and *Cocconeis costata* make up a smaller contribution. Only a few pelagic diatoms are evident (*Chaetoceros* spores). The following station on this transect is 52, which has been discussed above as part of transect A.

Station 54 has one of the highest percentages of *Chaetoceros* spp. spores of all the sample sites. This genus has been used at high latitudes to indicate high productivity (Sancetta 1982). Twenty-five percent of the total flora is comprised of pelagic diatoms, dominated by *Chaetoceros* spp. spores, *Nitzschia grunowii*, and *Thalassiosira* spp., including a few specimens of *T. gravida*. By far the most important benthic species is *Navicula ammophila* with *Cocconies costata* and *Achnanthes* spp. as minor components of the flora. This is an expected pattern of benthic diatoms versus pelagic diatoms, since the station is one of the westernmost sample locations, and experiences marine conditions more directly. Also, the percentage of pelagic diatoms species correlate well with depth, which increases along the transect towards the sea.

pelagic diatoms (45 %). *Chaetoceros* spores account for the greatest percentage (24 %) followed by *Thalassiosira* group as well as *N. grunowii*. Benthic diatoms still make up a sizeable portion of the total assemblage (Fig. 4A, Table 2). The water depth at site 60 is 48 m, and, given the turbid water with shallow photic zone, the benthic diatoms have probably been washed out from shallower areas. Thus, as the marine influence increases further away from the ice front, the percentage of marine pelagic diatoms increases, probably in response to the lessening of the meltwater/marine water stratification and its in1by the pack-ice indicators *Nitzschia grunowii* and *N. cylindra* (Grun.) Hasle. *Chaetoceros* spp. are also frequent, as well as *Thalassiosira* spp. Of the benthic diatoms *Cocconeis costata*, *Gomphonema gracile* Ehrenberg, and *Opephora* spp. are the dominant species, with many other species present in smaller percentages (Table 1).

Late Quaternary Samples

Eight samples from a raised Late Weichselian emergence sequence on the north side of the fjord (Forman 1986) were analyzed for diatoms. Two samples which are analogous to modern fjord muds (i.e., samples 52 and 50, above), contained no traces of diatoms. Two other samples, approximately analogous to the sublittoral environment (similar to modern sample 46), also were devoid of diatoms. Another four samples from raised glacial-marine and sublittoral sediment, deposited during the penultimate deglaciation, were barren of diatoms as well, although they contained abundant benthic foraminifera (Lehman et al. 1986). It is likely that these sediment samples originally contained a diatom flora and that this may have been severely fragmented and dissolved. Diatom frustule fragmentation often takes place along coastlines and in shallow environments, and dissolution of diatom frustules has been reported in sediments exposed to air, especially in coarser sediments (Beyens and Denys 1982). This may facilitate dissolution of the diatom frustules. Beyens and Denys (1982) also report that fragmentation of frustules can result from compaction of sediments, presumably as they are dewatered and raised above the marine influence.

In this area of Spitsbergen, the bedrock often consists of dolomite, which maintains a relatively high pH of the interstitial waters (pH about 8–9). Groundwater and soil pH have been measured to be between 7.8 and 8.0 in this locality (Forman and Miller 1984), which might satisfy the geochemical conditions for the dissolution of biogenic silica (cf. Elgawharg and Lindsay 1972). However, according to Erez et al. (1982), dissolution of biogenic silica under marine conditions is primarily influenced by saturation and temperature, with low temperatures (1.5 C) significantly decreasing solubility. In the raised marine sections in Engelskbukta with its unusually high pH, the reason for absence of diatoms is probably a result of a combination of fragmentation of a relatively low number of diatoms compared to the number of sediment particles, and dissolution, as the sediment was raised above sea level.

Conclusions

On the basis of our investigation of the sediment and diatom assemblages in the Engelskbukta Fjord, we have arrived at the following conclusions:

(1) Diatom sediment assemblages were found in very close proximity (within 30 m–4 km) to the actively calving ice-margin of a tidewater glacier in Spitsbergen.

(2) Diatom concentration was relatively constant (and low) at distances about 30 m or more from the glacier front, except in one case (station 66).

(3) The large amount of sediment discharged both from the glacier and from other local meltwater-fed rivers does not prevent diatom productivity, or obscure diatom frustules.

The flora changes in composition from essentially 100 % benthic diatoms to 50 % benthic diatoms/50 % pelagic diatoms, as the sample distance from the snout and/or the shore increases (Figs. 4A, B). With very few exceptions, the diatom taxa were marine or brackish (Table 1).

(4) Sediment throughout the fjord is dominated by medium silt and clay, with negligible amounts of sand and coarser fractions.

(5) All eight Late Quaternary sediment samples were barren of diatoms, which is surprising considering that the raised marine section has similar particle size characteristics and is assumed to be analogous to the modern fjord sedimentary environments (Forman 1986). The lack of diatom frustules in these raised marine sediment very likely can be attributed to a combination of mechanical abrasion of the frustules with disturbance and dewatering of the sediment and dissolution.

Acknowledgements

We thank J. T. Andrews, S. Lehman, and G. H. Miller for discussions and for reviewing the manuscript. Jim Walters very ably assisted in the field; Norsk Polar Institutt and King Bay Coal Co., Spitsbergen, provided much appreciated support. This work was in part supported by NSF grants DPP 8303425 and DPP 8303624.

Literature Cited

ANDERSON, D. S., R. B. DAVIS, AND F. BERGE. 1986. Relationships between diatom assemblages in lake surface-sediments and limnological characteristics in southern Norway. Pp. 97–113 *in* Diatoms and Lake Acidity, J. P. Smol, R. W. Battarbee, R. B. Davis, and J. Merilainen, eds. Kluwer Academic Publishers, Boston.

BEYENS, L. AND L. DENYS. 1982. Problems in diatom analysis of deposits. Allochtonous valves and fragmentation. Geologie en Mijnbouw 61:159–162.

CHARLES, D. F. 1985. Relationships between surface sediment diatom assemblages and lakewater characteristics in Adirondack lakes. Ecology 66:994–1011.

CLARK, P. U., S. K. SHORT, K. M. WILLIAMS, AND J. T. ANDREWS. 1989. Late Quaternary chronology and Paleoenvironments of Square Lake, Torngat Mountains, Labrador. Can. J. Earth Sci. 26:2130– 2144.

ELVERHOI, A., A. LIESTOL, AND J. NAGY, J. 1980. Glacial erosion, sedimentation and microfauna in the inner part of Kongsfjorden, Spitsbergen. Saert. Norsk Polarinst. Skr. 172:33–58.

ELVERHOI, A., A. LONNE, AND R. SELAND. 1983. Glaciomarine sedimentation in a modern fjord environment, Spitsbergen. Polar Res. 1:127–149.

ELGAWHARG, S. M. AND W. L. LINDSAY. 1972. Solubility of silica in soils. Soil Sci. Soc. Am. Proc. 36:439–442.

EREZ, J., K. TAKAHASHI, AND S. HONJO. 1982. In-situ dissolution experiment of radiolaria in the central North Pacific Ocean. Earth Planet. Sci. Lett. 59:245–254.

FORMAN, S. L. 1986. Quaternary glacial, marine and soil developmental history of Forlansund area, western Spitsbergen, Svalbard. Ph.D. thesis, University of Colorado, Boulder. 300 pp.

———. 1990. Thermoluminescence properties of fiord sediments from Engelskbukta, Western Spitsbergen, Svalbard: a new tool for deciphering depositional environment? Sedimentology 35:377–384.

FORMAN, S. L. AND G. H. MILLER. 1984. Time dependent soil morphologies and pedogenic processes on raised beaches, Broggerhalvoya, Spitsbergen, Svalbard Archipolago. Arctic Alp. Res. 16:381–394.

HAMBREY, M. J. 1984. Sedimentary processes and buried ice phenomena in the proglacial areas of Spitsbergen glaciers. J. Glaciol. 30:116–119.

HORNE, E. P. W. 1985. Ice-induced vertical circulation in an arctic fiord. J. Geophys. Res. 90:1078–1086.

HUSTEDT, F. 1959. Die Kieselalgen Deutschlands, Osterreichs und der Schweiz. English translation, 1985, by Norman Jensen. Koeltz Scientific Books, Koenigstein. 918 pp.

JOUSE, A. P. 1962. Stratigraphic and paleogeographic investigations in the northwestern parts of the Pacific Ocean. Akademia Nauk, SSSR, Institute of Oceanography, Moscow. 258 pp.

LEHMAN, S. J., G. H. MILLER, AND H.-P. SEJRUP. 1986. Late Quaternary foraminiferal and stable isotope stratigraphy, West Spitsbergen, Svalbard. Geol. Soc. Am. Abst. 18:670.

MAHER, L. J. 1980. Statistics for microfossil concentration measurements, employing samples spiked with marker grains. Rev. Paleobot. Palynol. 32:153–191.

MARTIN, J. H., R. M. GORDON, AND S. E. FITZWATER. 1990. Iron in Antarctic waters. Nature 345:156–158.

MCDONALD, R. W., C. S. WONG, AND P. E. ERICKSON. 1987. The distribution of nutrients in the southeastern Beaufort Sea: Implications for water circulation and primary productivity. J. Geophys. Res. 92:2939–2952.

PARKER, B. S., L. E. HEISKELL, AND W. J. THOMPSON. 1978. Non-biogenic fixed nitrogen in Antarctica and some eclolgical implications. Nature 271: 651–652.

SANCETTA, C. 1982. Distribution of diatom species in surface sediments of the Bering and Okhotsk seas. Micropaleont. 28:221–257.

TYNNI, R. 1978. Uber Finnlands rezente und subfossile Diatomeen, X. Geol. Surv. Finnland, Bull. 296:1–55. '63

WILLIAMS, K. M. 1986. Recent Arctic marine diatom assemblages from bottom sediments in Baffin Bay and Davis Strait. Mar. Micropaleont. 10:327–341.

———. 1990a. Paleolimnology of three Jackman Sound lakes, southern Baffin Island, based on down-core diatom analyses. J. Paleolimnol. 4:203–217.

——— 1990b. Late Quaternary paleo-oceanography of the western Baffin Bay region: Evidence from fossil diatoms. Can. J. Earth Sci. 27:1487–1494.

ZELLER, E. J., G. DRESCHOFF, AND M. D. TURNER. In Press. Impact of ice related plant nutrients on glacial margin environments. *In* Archaeological Sediments in Context, J. K. Stein and W. R. Farrand, eds. Center for the Study of Early Man, Institute for Quaternary Studies, University of Maine at Orono.

Ultrastructure of Some Interesting and Stratigraphically Significant Diatom Taxa From the Upper Paleocene to Lower Eocene Sediments of ODP Site 752, Eastern Indian Ocean

by

Elisabeth Fourtanier[1]

Laboratoire d'Hydrologie et de Géochimie Isotopique,
Université Paris-Sud, 91405 Orsay Cedex, France
and U.S. Geological Survey, Menlo Park, California 94025

and

Robert Oscarson

U. S. Geological Survey, Menlo Park, California 94025

with 5 plates

Abstract: Well-preserved diatom assemblages were recovered from Upper Paleocene to Lower Eocene sediments at the eastern Indian Ocean ODP Site 752. The ultrastructure of some interesting and stratigraphically useful taxa has been investigated under the scanning electron microscope. The studied taxa include: *Stellarima* spp., *Thalassiosiropsis wittiana* (Pantocsek) Hasle, *Triceratium orbiculatum* Schibkova, *Trinacria aries* Schmidt, *Hemiaulus peripterus* var. *peripterus* Fenner, *H. peripterus* var. *longispinus* Fourtanier, and *Hemiaulus incurvus* Schibkova.

Introduction

Although Paleocene and Early Eocene diatoms have been documented from various localities of the former U. S. S. R. (e.g., Krotov and Schibkova 1959; Jousé 1979), their occurrence is very uncommon in the deep sea record (see Fourtanier 1991 for a review of the literature). A thick sequence of Upper Paleocene to Lower Eocene diatom-bearing sediments was recovered at Broken Ridge ODP (Ocean Drilling Program) Site 752

[1]Current address: Diatom Collection, Department of Invertebrate Zoology and Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.

(30°53'S, 93°35'E) in the eastern Indian Ocean. Site 752 is of great interest because: (1) it contains the longest sequence of Upper Paleocene and Lower Eocene diatomaceous sediments known in the deep sea record (about 180 m of sediments ranging in age between 63 and 55 Ma); (2) it is the first deep-sea site known to contain diatoms across the Paleocene-Eocene boundary; and (3) the ages are well constrained by magnetostratigraphy, coccolith and foraminifer stratigraphies.

An earlier study of the diatoms at Site 752, based on light microscope (LM) observations, included documentation of the diatom assemblages throughout the section, description of three new taxa, and the proposal of a diatom zonation for the Paleocene to Early Eocene time interval (Fourtanier 1991). Only limited observations were completed for that publication under the scanning electron microscope (SEM).

The ultrastructure of Early Paleogene diatom species is of interest for both taxonomy and evolution, as most of these earlier taxa are extinct today. A few authors have documented Early Paleogene diatoms under the SEM (e.g., Mukhina 1974; Jousé 1977; Sims and Ross 1988; Sims 1989); however, the ultrastructure of many of these earlier diatoms is still largely unexplored. This paper investigates the ultrastructure of some selected species from Site 752 and focuses on stratigraphically significant taxa.

Materials and Methods

Carbonate and organic matter were removed by boiling the sediment with HCl and H_2O_2. Residues were rinsed by washing in distilled water (see Fourtanier 1991). A strewn sample was then mounted with a pipette on a cover slide, dried overnight and attached to a metal stub using a silver paint. Gold/Palladium (60/40) coated diatom residues were examined using a Cambridge Stereoscan 250 Mk2 scanning electron microscope. Coating thickness was approximately 20 nanometers. During SEM operations, the sample was tilted 20–70 degrees and acceleration voltage was 15 and 20 KV.

Results and Discussion

SEM photomicrographs of selected diatom taxa from Site 752 are presented in Figures 1–27. The ultrastructure of some of these taxa will be discussed and comments on their stratigraphic occurrences will be given.

Stellarima spp.
(Figs. 1–4)

The genus *Stellarima* Hasle & Sims is characterized by "circular valve outline, rimoportulae positioned near or at the valve center, loculate areolae with internal foramina and external cribra interrupted by occasional specialized pores (observable on the valve exterior only)" (Hasle and Sims 1986).

Two *Stellarima* taxa, designated *S.* sp. 1 and *S.* sp. 2, have been recorded from Site 752 (Fourtanier 1991) that have similar areolae patterns. The taxa differ in the number of central labiate processes; *Stellarima* sp. 1 includes smaller forms (17–48 µm diameter) with one single central labiate process, *S.* sp. 2 includes larger forms (39 to at least 150 µm in diameter) with at least two central labiate processes (commonly 2 or 3, as many as 7). The areolae, 8–11/10 µm for *S.* sp. 1 and 5–11/10 µm for *S.* sp. 2, vary in size between specimens, and also within individual valves with larger areolae located near the center. This difference in areolae size from the center to the margin of the valve is particularly marked in larger specimens (*S.* sp. 2). For both taxa, areolae are arranged in curved tangential rows; however, on some of the largest specimens, a somewhat fascicu-

lated pattern is superimposed on the tangential pattern. The external velum and the specialized pores were not observed due to dissolution of the valve. When comparing *S.* sp. 1 and *S.* sp. 2, an apparent relationship exists between the size of the valve and the number of labiate processes present; this would suggest that *S.* sp. 1 and *S.* sp. 2 may belong to the same taxon. This hypothesis still has to be tested, however, it is consistent with the similarities in stratigraphic ranges of these two forms at Site 752, namely, sporadic occurrence in the lowermost Eocene and consistent occurrence in the Upper Paleocene (Fourtanier 1991).

Stellarima sp. 1 (Figs. 1–2) resembles specimens described as resting spores of *S. steinyi* (Hanna) Hasle & Sims from various localities of Late Cretaceous age and illustrated in Sims and Hasle (1987), both for the presence of a single central labiate process and similarities in pore size. *Stellarima steinyi*, however, is larger (30–165 µm diameter) than *S.* sp. 1 and differs mostly by the areolae pattern, with fascicles of radial rows for *S. steinyi* and curved tangential rows for *S.* sp. 1. The Oligocene species *S. primalabiata* (Gombos) Hasle & Sims (see Gombos and Ciesielski 1983) resembles *S.* sp. 1 by its single labiate process and its areolae pattern (''areolae in tangential rows with secondary marginally concave rows''). *Stellarima primalabiata* is, however, typically larger (diameter is 66 µm on average) than *S.* sp. 1, and has pores uniform in size (7–8/10 µm).

Stellarima sp. 2 (Figs. 3–4) resembles the resting spore of the modern Antarctic species *S. microtrias* (Ehrenberg) Hasle & Sims (Hasle and Sims 1986), in valve diameter, pore size, and number of central processes; however, *S.* sp. 2 differs from that species by the areolar pattern, which is fasciculate in *S. microtrias* and tangential in *S.* sp. 2.

Fenner (1991) reports the genus *Stellarima* from the Paleocene of the South Atlantic with the occurrence of two species: *S. primalabiata* and *S. microtrias*, but does not provide illustrations. It would be interesting to compare her material with material of similar age from Site 752, as it is possible that *S. primalabiata* and *S. microtrias* of Fenner (1991) may be identical to *S.* sp. 1 and *S.* sp. 2 of Fourtanier (1991).

In conclusion, although very similar in morphology, the *Stellarima* species reported from various ages (Cretaceous to Holocene) have clear differences when considered in greater detail. This indicates a potential stratigraphic significance for species of this genus and suggests the need for detailed observation and description when documenting *Stellarima* species from fossil localities.

Hyalodiscus scoticus (Kützing) Grunow
(Figs. 5, 6)

An internal view and detail of a marginal labiate process in *Hylaodiscus scoticus* are illustrated in Figures 5 and 6, respectively.

Thalassiosiropsis wittiana (Pantocsek) Hasle
(Figs. 7–10)

The specimen illustrated in Figures 7–10 meets the characteristics of the genus *Thalassiosiropsis* Hasle by having loculate areolae with internal cribra, external foramina in straight tangential rows, cribral pores radially oriented, and a central ''multistrutted process'' (Hasle and Syvertsen 1985). It is identified as *T. wittiana* (Pantocsek) Hasle on the basis of similarities in valve diameter, size, structure, and arrangement of the areolae. Most of the specimens of *T. wittiana* illustrated in Hasle and Syvertsen (1985) have a internal funnel-shaped central multistrutted process with linked struts. Other specimens, however, are similar to those of Site 752 with the multistrutted process composed of short and independent struts (Hasle and Syvertsen 1985: Figs. 27–28, 31, 32); this may be the

result of the multistrutted process being reduced to the base of each strut (P. A. Sims, pers. comm., 1991).

Thalassiosiropsis wittiana has been reported from the Upper Cretaceous to the Lower Eocene in the former U. S. S. R., the Upper Cretaceous of California (Hasle and Syvertsen 1985), and from the Upper Paleocene of Site 752 (Fourtanier 1991). *Thalassiosiropsis*, very likely an extinct genus, is a possible ancestor of the genus *Thalassiosira* (Hasle and Syvertsen 1985).

"Triceratium" orbiculatum Schibkova *in* Krotov and Schibkova
(Figs. 11–12)

"*Triceratium*" *orbiculatum* Schibkova is a large species, with radial arrangement of areolae, and is easy to recognize under both the SEM and light microscope. The central part of the valve, which is circular in shape, is surrounded by a sulcus (Fig. 12), most developed near the apical projections. Small chambers are formed by inward extensions of the sulcus. Smaller pores are present between larger areolae.

"*Triceratium*" *orbiculatum* occurs in the uppermost Paleocene and lowermost Eocene of Site 752 (ca. 59 to 55 Ma). It was originally described from the Paleogene of the Urals (Krotov and Schibkova 1959).

"Triceratium" sp. cf. *Triceratium gombosii* Fenner
(Figs. 13, 14)

An external view of this taxon is shown in Figures 13 and 14.

"*Triceratium*" *orbiculatum* and "*Triceratium*" sp. cf. *gombosii* are not true *Triceratium* species. They possibly belong to the genus *Sheshukovia* Glezer (see Round et al. 1990).

Trinacria aries Schmidt
(Figs. 15, 16)

Trinacria aries Schmidt (Figs. 15, 16) has triangular valves with slightly concave sides and rounded apices. Valves are coarsely areolated (ca. 2–3 areolae in 10 µm), and smaller pores are present between areolae. Externally (Fig. 15), a well-developed marginal ridge is continuous between the apical elevations. Summits of the elevations are flat, finely punctate, and surrounded by triangular spines.

At Site 752, *T. aries* has its last occurrence at about 57.8 Ma, near the Paleocene-Eocene boundary (Fourtanier 1991) and may be a useful stratigraphic marker to recognize that boundary.

Hemiaulus peripterus Fenner
(Figs. 17–26)

The description of *Hemiaulus peripterus* var. *peripterus* Fenner (Figs. 17–21) was originally based on light microscope observations (Fenner 1984). Fenner indicated that valves appear structureless under the light microscope, but she recognized the presence of a "round, slightly elevated structure" at the center of the valve. This species is also characterized by downward acute extensions of the mantle at the valve poles. *Hemiaulus peripterus* is here documented for the first time with the SEM (Figs. 17–21). The valve is generally free of punctations, however, small pores are present on the apical elevations and are more dense near the spines (Figs. 18, 21). A crenulated ridge runs around the valve (Figs. 17–20). There is an elongated cavity underneath the valve (Fig. 17), which deepens at the center, forming a rounded depression. A process (probably a labiate process) is present at the center of that depression (Figs. 17, 19). Apical elevations seem to be

partially hollow (Fig. 20). An elongated cavity is also present on the upper part of the valve (Fig. 18) with the central part slightly domed and bearing a small tube (not illustrated here), which is the external opening of the labiate process.

Hemiaulus peripterus var. *longispinus* Fourtanier (Figs. 22–26) was described from the sediments of Site 752 (Fourtanier 1991). It differs from the nominate variety by longer downward acute extensions and straighter valves. Specimens examined from Site 752 are not well preserved and the apical elevations, which are partially dissolved, could not be observed. As with *H. peripterus* var. *peripterus*, elongated cavities are present on the upper part (Fig. 24) and on the lower part of the valve (Figs. 25, 26). A rounded depression is present at the center of both upper and lower cavities. A process could not be observed, due probably to poor preservation.

The presence of downward apical extensions at the poles is a character somewhat unusual among *Hemiaulus* species. The Eocene and Oligocene species *H. caracteristicus* Hajós, and the Eocene species *H. prolongatus* Ross & Sims share this character. *Hemiaulus caracteristicus* resembles *H. peripterus* var. *peripterus* with its almost hyaline valves with minute pores on the horns (see Gombos and Ciesielski 1983). It differs from that species, however, by lacking a central structure. *Hemiaulus prolongatus* resembles *H. peripterus* var. *longispinus* with its strongly developed acute downward extensions; it differs from that species, however, by the presence of large areolae on the mantle and the apical elevations (see Ross et al. 1977). According to Round et al. (1990), a diagnostic character for the genus *Hemiaulus* Ehrenberg relative to other, similar genera is the presence of one apical spine at the end of each of the two elevations. *Hemiaulus peripterus*, *H. caracteristicus*, and *H. prolongatus* have such spines and, therefore, seem to be correctly classified within the genus *Hemiaulus*.

Recent SEM observations of intact specimens of *Hemiaulus caracteristicus* (Mahood et al. 1993) suggest that in our specimens of *Hemiaulus peripterus*, only the more heavily silicified remains of the valve are preserved. A more delicate mantle structure might have existed between the downward extensions as it is observed in *Hemiaulus caracteristicus*.

The "*peripterus-caracteristicus*" group may be stratigraphically significant. *Hemiaulus peripterus* var. *peripterus* is known to occur in numerous sections of Early and Late Paleocene age (Fenner 1991). At Site 752, it ranges from the Early and Early-Late Paleocene, up to 61.6 Ma (Fourtanier 1991). Its first occurrence defines the base of the Paleocene *H. peripterus* Zone of Fourtanier (1991). At Site 752, *H. peripterus* var. *longispinus* ranges from the earliest Eocene, down to 57.1 Ma (Fourtanier 1991). *Hemiaulus caracteristicus* occurs in the Eocene and Oligocene (Fenner 1984). *Hemiaulus prolongatus* occurs in the middle and Upper Eocene (i.e., in VEMA cruise 17 core 107 and VEMA cruise 18 core 104, according to P. A. Sims, pers. comm., 1991; for dating see Ross and Sims 1985).

Hemiaulus incurvus Schibkova in Krotov and Schibkova
(Fig. 27)

Hemiaulus incurvus Schibkova is a large, heavily silicified, and coarsely punctate species. Its wide distribution in Upper Paleocene sediments throughout the world makes it a useful stratigraphic marker. *Hemiaulus incurvus* ranges between 61.6 and 56.7 Ma (Late Paleocene and earliest Eocene) at Site 752 (Fourtanier 1991). Its first occurrence defines the Late Paleocene *Hemiaulus incurvus* Zone of Fourtanier (1991).

Acknowledgements

Samples were supplied through the assistance of the International Ocean Drilling Program. E. F. thanks ODP France and INSU for providing financial support and the U. S. G. S. for providing space and facilities. The manuscript benefitted from the reviews of Patricia A. Sims, John A. Barron, and Lisa D. White as well as the careful editing of J. Patrick Kociolek.

Literature Cited

FENNER, J. 1984. Eocene-Oligocene planktic diatom stratigraphy in the low latitudes and the high southern latitudes. Micropaleontology 30:319–342.

———. 1991. Stratigraphy and paleo-oceanographic implications of Paleocene diatoms from ODP Leg 114. Pp. 123–154 *in* Proceedings of the Ocean Drilling Program, Scientific Results, 114, P. F. Ciesielski and Y. Kristoffersen, eds. Ocean Drilling Program, College Station, Texas.

FOURTANIER, E. 1991. Paleocene and Eocene diatom biostratigraphy and taxonomy of eastern Indian Ocean Site 752, ODP Leg 121. Pp. 171–187 *in* Proceedings of the Ocean Drilling Program, Scientific Results, 121, J. Peirce and J. Weissel, eds. Ocean Drilling Program, College Station, Texas.

GOMBOS, A. M. Jr. AND P. F. CIESIESELKI. 1983. Late Eocene to Early Miocene diatoms from the southwest Atlantic. Pp. 583–634 *in* Initial Reports of the Deep Sea Drilling Project, 71, Pt. 2, W. J. Ludwig and V. A. Krasheninnikov, eds. U. S. Govt. Printing Office, Washington D. C.

HASLE, G. R. AND P. A. SIMS. 1986. The diatom genera *Stellarima* and *Symbolophora* with comments on the genus *Actinoptychus*. Br. phycol. J. 21:97–114.

HASLE, G. R. AND E. E. SYVERTSEN. 1985. *Thalassiosiropsis*, a new diatom genus from the fossil records. Micropaleontology 31:82–91.

JOUSÉ, A. P. 1977. Atlas of microorganisms in bottom sediments of the oceans (diatoms, radiolarians, silicoflagellates, coccoliths). Nauka, Moscow, 196 pp.

———. 1979. Diatom biostratigraphic zones of the Eocene. Nova Hedwigia, Beih. 64:427–445.

KROTOV, A. I. AND K. G. SCHIBKOVA. 1959. New species of diatoms from Paleogene deposits in the Urals. Botanicheskie materialy otdela sporovykh rastenii, Botanicheskie Institut, Akademia Nauk SSSR 12:112–129.

MAHOOD, A.D., J.A. BARRON AND P.A. SIMS. 1993. A study of some unusual, well preserved Oligocene diatoms from Antarctica. Nova Hedwigia, Beih. 106:243-267.

MUKHINA, V. V. 1974. The Paleocene diatom ooze in the eastern part of the Indian Ocean. Okeanologiya 14:852–858.

ROSS, R. AND P. A. SIMS. 1985. Some genera of the Biddulphiaceae (diatoms) with interlocking linking spines. Bull. Br. Mus. (Nat. Hist.), Bot. Ser. 13:277–381.

ROSS, R., P. A. SIMS, AND G. R. HASLE. 1977. Observation on some species of the Hemiauloideae. Nova Hedwigia, Beih. 54:179–213.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms, Biology and Morphology of the Genera. Cambridge University Press, Cambridge. 747 pp.

SIMS, P. A. 1989. Some Cretaceous and Paleocene species of *Coscinodiscus*: a micromorphological and systematic study. Diatom Res. 4:351–371.

SIMS, P. A. AND G. R. HASLE. 1987. Two Cretaceous *Stellarima* species: *S. steinyi* and *S. distincta*: their morphology, palaeogeography and phylogeny. Diatom Res. 2:229–240.

SIMS, P. A. AND R. ROSS. 1988. Some Cretaceous and Palaeogene *Trinacria* (diatom) species. Bull. Br. Mus. (Nat. Hist.), Bot. Ser. 18:275–322.

Explanation of Plates

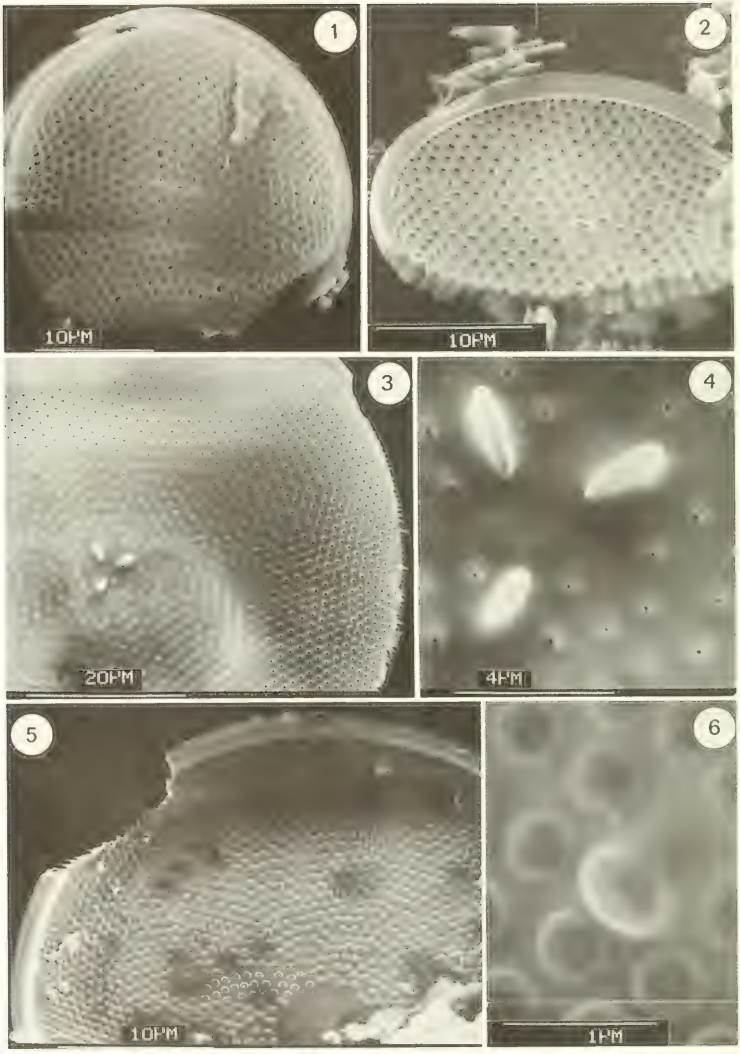
Plate 1, Figures 1–6
FIGURES 1, 2. *Stellarima* sp. 1 (Sample 752A-29X-3, 55–57 cm). FIGURE 1. External view. FIGURE 2. Internal view; note the presence of a single central labiate process. FIGURES 3, 4. *Stellarima* sp. 2 (Sample 752A-29X-3, 55–57 cm), FIGURE 3. Internal view. FIGURE 4. Detail of the three central labiate processes. FIGURES 5, 6. *Hyalodiscus scoticus* (Kützing) Grunow (Sample 752A-22X-3, 55–57 cm). FIGURE 5. Internal view. FIGURE 6. Detail of a marginal labiate process.

Plate 2, Figures 7–10
FIGURES 7–10. *Thalassiosiropsis wittiana* (Pantocsek) Hasle (Sample 752A-29X-3, 55–57 cm). FIGURE 7. Internal view, detail of a broken part of the valvar disc. Note the internal cribra and external foramina. FIGURE 8. Detail of the margin. FIGURE 9. General view. FIGURE 10. Detail of the central part of the valve with the multistrutted process and central areolae with few or no cribral pores.

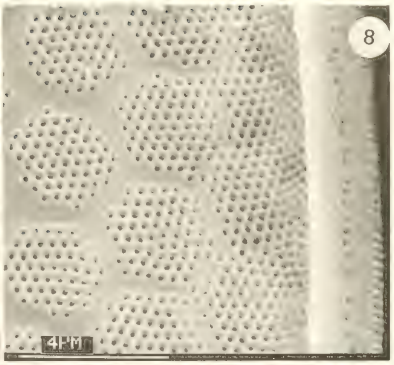
Plate 3, Figures 11–16
FIGURES 11, 12. "*Triceratium*" *orbiculatum* Schibkova (Sample 752A-18X-CC). FIGURE 11. External view. FIGURE 12. Internal view. FIGURES 13, 14. "*Triceratium*" sp. cf. *T. gombosii* Fenner (Sample 752A-22X-3, 55–57 cm). FIGURE 13. External view. FIGURE 14. Detail of the central spines. FIGURES 15, 16. *Trinacria aries* Schmidt (Sample 752A-29X-3, 55–57 cm). FIGURE 15. External view. FIGURE 16. Internal view.

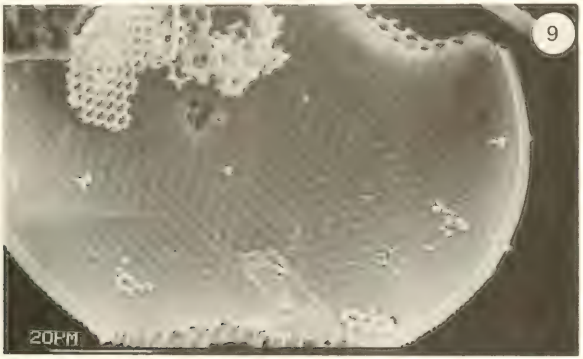
Plate 4, Figures 17–21
FIGURES 17–21. *Hemiaulus peripterus* var. *peripterus* Fenner (Sample 752A-29X-3, 55–57 cm). FIGURES 17, 18. Oblique and marginal view, respectively, of the same specimen. FIGURES 19, 20. Detail of the elongate cavity underneath the valve. FIGURE 19. Center of the valve; a labiate process is present at the center of a rounded depression. FIGURE 20. The apical elevation seems to be at least partly hollow. FIGURE 21. Detail of apical elevation; note the small poroids.

Plate 5, Figures 22–27
FIGURES 22, 23. *Hemiaulus peripterus* var. *longispinus* Fourtanier (Sample 752A-18X-CC). FIGURE 22. General view. FIGURE 23. Detail of elevation/spine junction. FIGURES 24–26. *Hemiaulus peripterus* var. *longispinus* Fourtanier (another specimen, Sample 752A-18X-CC). FIGURE 24. Specimen tilted at 70° (view of the upper part of the valve). FIGURES 25, 26. Same specimen tilted at 70° in the other direction. FIGURE 25. Detail of the lower part of the valve. FIGURE 26. Detail of the central cavity. FIGURE 27. *Hemiaulus incurvus* Schibkova (Sample 752A-26X-1, 55-57cm).

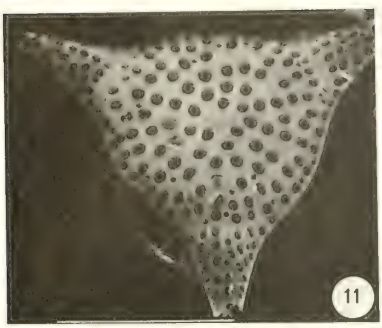

1
10PM
2
10PM
3
20PM
4
4PM
5
10PM
6
1PM

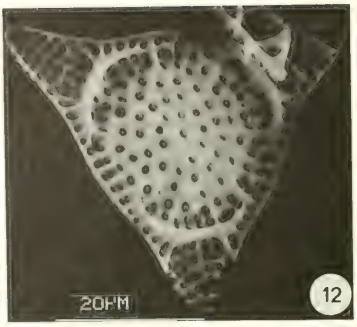
7
10PM

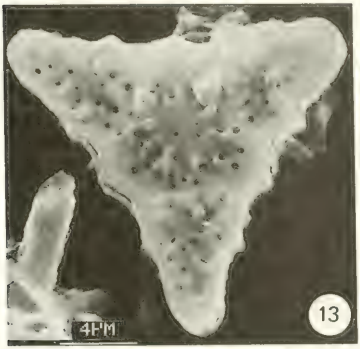

8
4PM

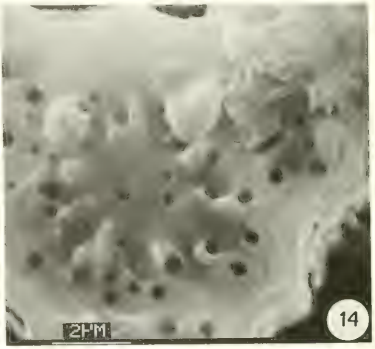

9
20PM

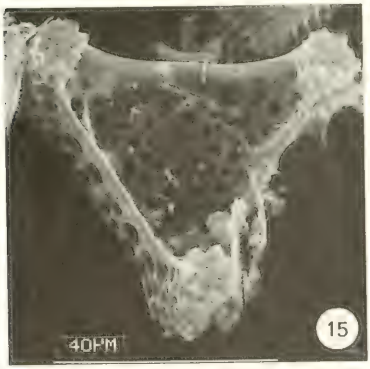
10
4PM


11

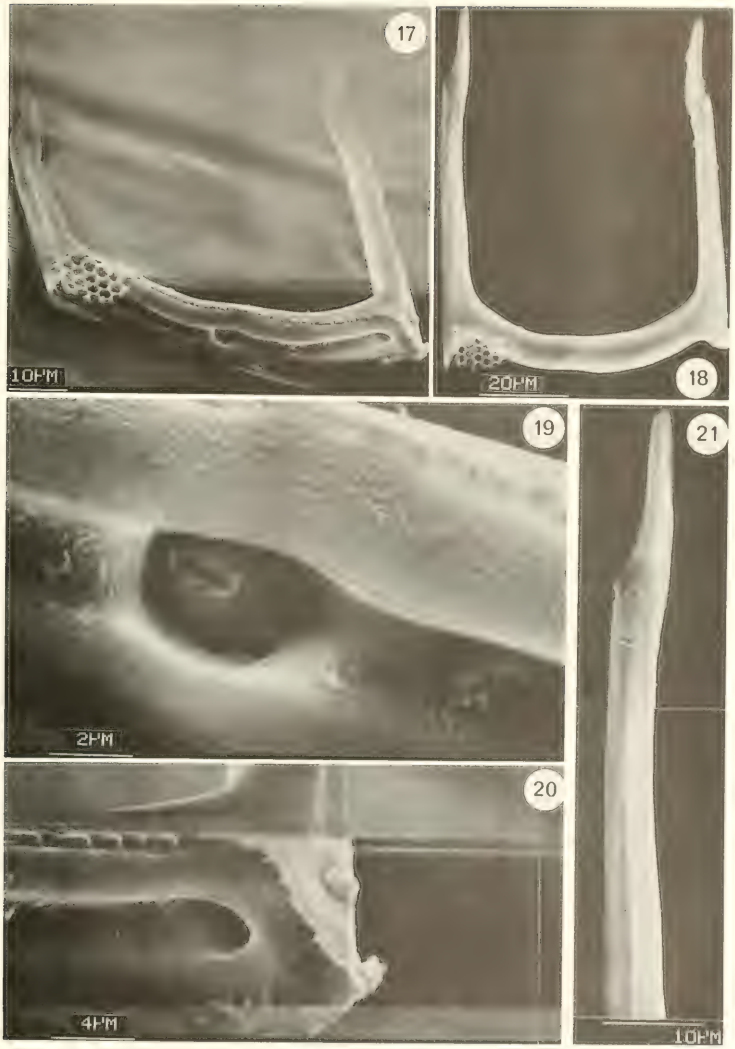

20PM
12

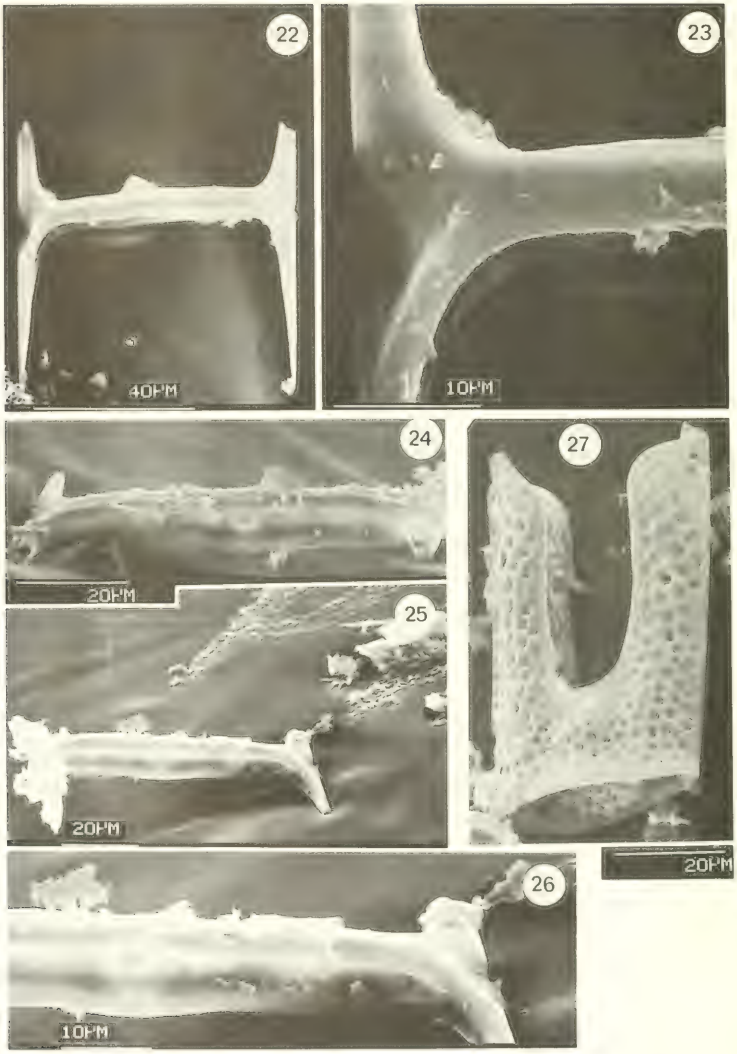

4PM
13


2PM
14


40PM
15

20PM
16


17
10µm
18
20µm
19
2µm
20
4µm
21
10µm


22
40PM
23
10PM
24
20PM
25
20PM
27
20PM
26
10PM

Diatom Biostratigraphy of Chert Intervals In the Miocene Monterey Formation at Pt. Reyes, Pt. Año Nuevo, Mussel Rock, and Lions Head, California

by

Lisa D. White

Department of Geosciences, San Francisco State University,
San Francisco, California 94132

with 6 figures and 4 tables

Abstract: The Monterey Formation exposed at Pt. Reyes, Pt. Año Nuevo, Mussel Rock, and Lions Head, California, consists mainly of porcelanite and black quartz chert interbedded with mudstone, siltstone, and dolomite. Diatom biostratigraphic analysis of the four sections, made possible by the recovery of diatom frustules from dolomite beds, has resulted in improved age estimates. The Monterey Formation at Pt. Reyes and Pt. Año Nuevo is similar in age and ranges from approximately 15.0–13.4 Ma and 14.7–13.7 Ma, respectively. The age of the base of the Pt. Reyes and Pt. Año Nuevo sections strongly contrasts with the age of the base of chert-bearing intervals at Mussel Rock and Lions Head in the Santa Maria basin, where diatom biostratigraphy suggests an age at least 2 million years younger than intervals in the north-central California basins. The chert interval at Mussel Rock is between 12.7 and 8.9 Ma, and at the Lions Head section is approximately 11.4–9.2 Ma.

Introduction

The Monterey Formation of California is widely recognized for its abundant siliceous rocks, in particular its diatomites and diatomaceous mudstones (Pisciotto and Garrison 1981 and references therein). A large volume of the siliceous facies in coastal basins of California (Fig. 1), however, consists of the burial diagenetic products of diatomite and diatomaceous mudstone: chert, porcelanite, and siliceous shale. Considerable attention has been paid to chert-bearing intervals of the siliceous facies because of their tendency to form fractured petroleum reservoirs in basins such as the Santa Maria Basin (Redwine 1981; Roehl 1981; MacKinnon 1989). Because of the dissolution of diatoms during silica diagenesis, however, biostratigraphic estimates of the cherty intervals are severely lacking.

Preservation of diatom frustules within dolomite layers and concretions offers the potential for accurate chronostratigraphic dating of cherty intervals (Lagle 1984; Wornardt 1986; White 1989). Dolomite or dolostone is a common ancillary lithology in cherty sections. Diatom preservation occurs when the dolomite forms relatively early, before silica

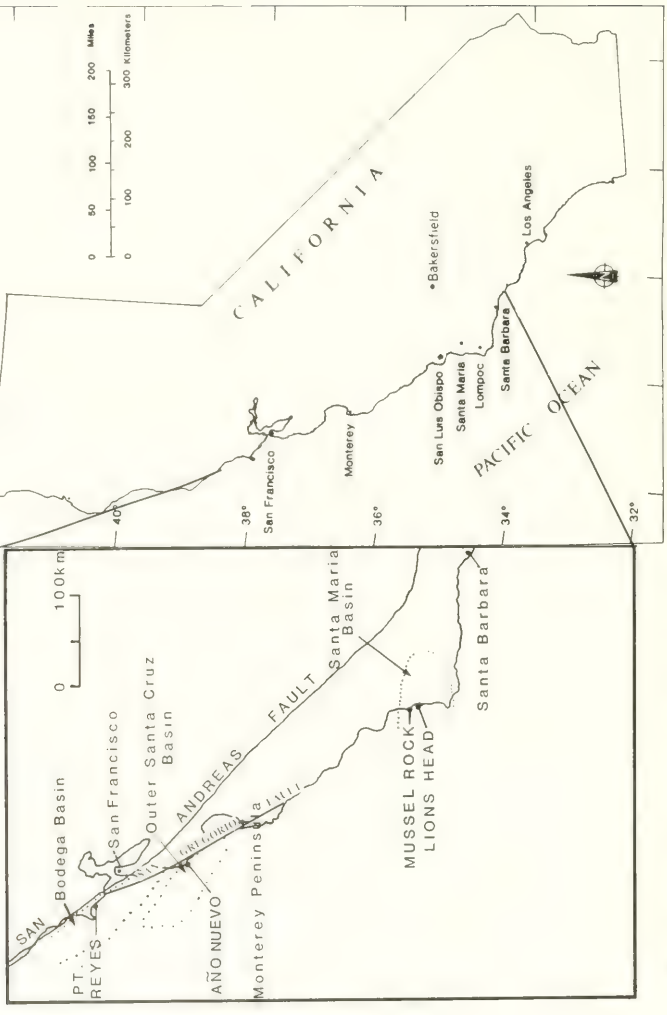


FIGURE 1. Location map of the Neogene coastal basins in California and the chert-bearing sections discussed in this report.

diagenesis (Baker and Kastner 1981; Kastner et al. 1984), thereby protecting the delicate diatom frustules from dissolution during subsequent burial diagenesis. Both good age resolution and the synchroneity of diatom events across paleoenvironmental boundaries have made diatoms a very reliable group for chronostratigraphic investigations of the Monterey Formation (Barron 1986a, b). In the present report four chert intervals of the Monterey Formation were investigated at Pt. Reyes, Pt. Año Nuevo, Mussel Rock, and Lions Head (Fig. 1) in order to obtain more reliable estimates of their ages.

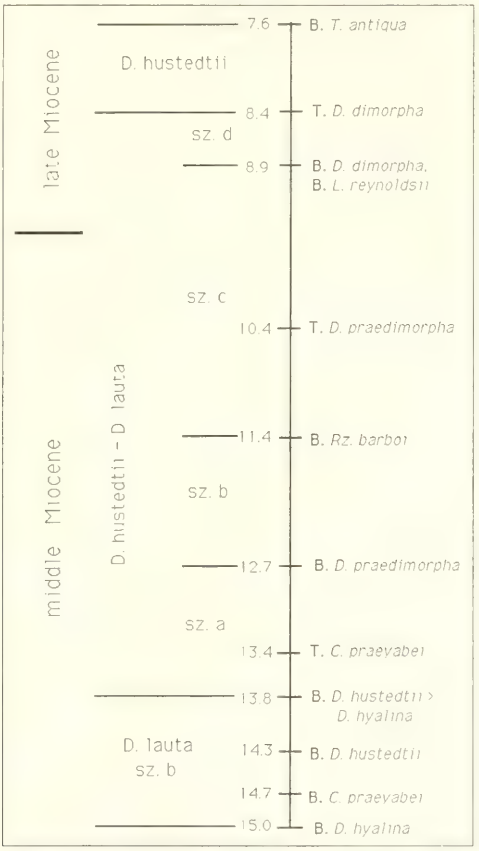


FIGURE 2. Diatom zonation for the Middle and Late Miocene from Barron (1986a) showing the primary and secondary datum levels. B = base of species range, T = top of species range. Ages are in Ma. Modified after Figure 2 of Barron (1986a).

Materials and Methods

Approximately 5–10 cc of dolomite were crushed with a rock hammer into fine granules. The sample was then heated in a solution of 10–20 ml of 30 % H_2O_2 for approximately 15–30 minutes, or until the reaction ceased. Then 25–50 ml of concentrated HCL and HNO_3 (aqua regia) were added, and the solution was heated for 30–60 minutes, or until the larger granules were broken up. If the sample did not disaggregate well, it was left in aqua regia overnight. The sample was then neutralized in 50–100 ml of 5 % NaOH for 15–30 minutes, and after cooling was filled with distilled water and left to settle for at least 2 hours. After centrifuging, the insoluble residue was strewn onto a cover slip and mounted to a slide with Hyrax.

All of the slides were examined for diatoms and the complete diatom taxon lists, along with abundance and preservation information are discussed more fully in White (1989). The diatom lists in Tables 1–4 show only the age-diagnostic species that allowed application of the diatom biostratigraphy of Barron (1986a) (Fig. 2).

Results

Pt. Reyes

The Monterey Formation at Pt. Reyes is structurally complex, and accurate stratigraphic section measurements and correlation are difficult to obtain. White (1989) measured several sections and two of those, one from the Santa Maria Beach area of Pt. Reyes and one from the Kelham Beach area, are highlighted here (Fig. 3).

The most common lithology in the section is cherty porcelanite and black chert that is interbedded with phosphatic mudstone and siltstone, and dolomite. The measured section at Santa Maria Beach starts at the stratigraphically lowest exposed dolomite bed within the siliceous facies. Diatom assemblages recovered and examined from the dolomites are shown in Tables 1a and 1b. Overall, diatoms are rare in dolomites sampled at the Pt. Reyes sections and show poor to moderate preservation. At the Santa Maria Beach section they include *Denticulopsis lauta*, *D. hyalina*, and *Coscinodiscus praeyabei*, characteristic of *D. lauta* subzone b (Table 1a), that ranges in age from 15.0–13.8 Ma. Reconnaissance samples taken from the Monterey Formation in the Kelham Beach area, where the Monterey Formation is unconformable overlain by the Santa Margarita Formation (Fig. 3), also yielded age diagnostic diatoms (Table 1b). The presence of *D. hustedtii*, *D. hyalina*, *D. lauta*, and *C. praeyabei* in sample number 87-PR-R2, and *C. praeyabei* in sample number 87-PR-R1 suggests that the section is part of either the *D. lauta* subzone b or *D. hustedtii-D. lauta* subzone a and has an age range between 14.7 and 13.4 Ma (White 1989, 1990).

Año Nuevo

The cherty interval at Año Nuevo consists mainly of opal-CT porcelanites, opal-CT cherts, and quartz cherts rhythmically interbedded with organic-rich mudstones and laminated dolomite beds (Fig. 4). In a section that dips to the northeast of a prominent anticline at Año Nuevo, the Monterey Formation was measured and sampled in detail. The base of the cherty interval overlies a prominent fault called the Año Nuevo thrust fault (Clark, 1981), and the top of the section is marked by the unconformable contact with the overlying Purisima Formation (Fig. 4).

Diatoms from the base of the NE section are characteristic of *D. lauta* subzone b and have an age range of 15.0 Ma–13.8 Ma. Dolomite sample AN-1, located approximately

Tables 1A and 1B. List of age diagnostic diatoms in Pt. Reyes showing stratigraphic interval of the samples and the diatom zones. Diatom zonation is after Barron (1986a).

TABLE 1A. Santa Maria Beach area.

Sample	Strat. interval (m)	Diatom zone	Age (Ma)	*Coscinodiscus praeyabei*	*Denticulopsis hustedtii*	*D. hyalina*	*D. lauta*
87-PRD-10	40					X	
87-PRD-9	35		B				
87-PRD-8	30.22			X		X	X
87-PRD-7	19.22	*D. lauta* b	15.0 - 13.8			X	
87-PRD-6	11.72		B				
87-PRD-5	10.45		B				
87-PRD-4	8.32						X
85-PRD-1	0					X	X

B = barren of diatoms, NA = no age diagnostic species present

TABLE 1B. Kelham Beach

Sample	Strat. interval (m)	Diatom zone	Age (Ma)	*Coscinodiscus praeyabei*	*Denticulopsis hustedtii*	*D. hyalina*	*D. lauta*
87-KB-1							X
87-KB-2			B				
87-KB-3	See		NA				
87-KB-4	Figure 3	*D. lauta* b	14.7 - 13.4	X			
87-KB-5				X		X	X
87-KB-6			B				
87-KB-7				X		X	X
87-KB-8			B				

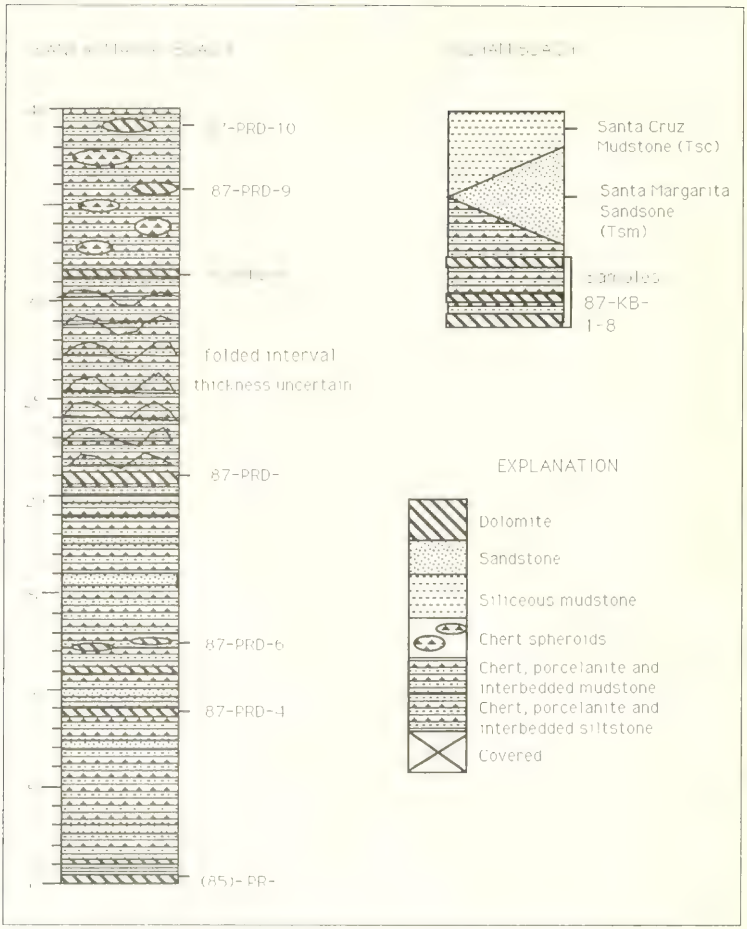


FIGURE 3. Lithostratigraphy of the Monterey Formation at the Santa Maria Beach and Kelham Beach sections, Pt. Reyes peninsula. Columns show stratigraphic position of samples collected, scale to the left of the column is in meters. Note that no scale is shown on the stratigraphic column for Kelham Beach because the sections were not measured in detail.

5 m from the fault contact (base of the section), contains *D. lauta* and *D. hyalina* (Table 2). Both of these species are continually present in dolomites sampled in the next 45 m of section that were not barren. Diatoms recovered from the top of the section yielded

TABLE 2. List of age diagnostic diatoms from the northeasterly dipping section at Año Nuevo showing stratigraphic interval of the samples and diatom zones.

Sample	Strat. interval (m)	Diatom zone	Age (Ma)	*Denticulopsis hustedtii*	*D. hyalina*	*D. lauta*
86-AND-115	54.4		13.8 —	X		X
86-AND-114	50.6				X	X
86-AND-113	46.1				X	X
86-AND-112	44.0		B			
86-AND-111	34.6	*D. lauta*	B			
86-AND-110	33.6				X	X
86-AND-109	31.7	b			X	X
86-AND-108	22.5		B			
86-AND-107	18.7				X	X
86-AND-106	17.4				X	X
86-AND-105	5.0		B			
AN-1	5.0		< 15.0		X	

B = barren of diatoms

TABLE 3. List of age diagnostic diatoms from the Mussel Rock section. Diatom zonation is after Barron (1986a).

Sample	Member	Diatom zone	Age (Ma)	*Actinocyclus ingens*	*Coscinodiscus praeyabei*	*Denticulopsis hustedtii*	*D. hyalina*	*D. katayamae*	*D. lauta*	*D. praedimorpha*	*Lithodesmium reynolsii*	*Rhizolenia barboi*
87-MRD-7A	Tmu	*D.hustedtii*				X		X				X
			— 8.4 —									
		d										
87-MRD-9A			— 8.9-8.2 —								X	
87-MRD-10A			NA									
87-MRD-11A			B									
87-MRD-12A	Tmm	c	NA									
87-MRD-12A*						X						
87-MRD-27						X						
87-MRD-26			— 10.4 —			X			X	X		
86-MRD-04		b				X				X		
86-MRD-06	Tml	a	— 12.7 —	X	X	X	X					
		D. hustedtii - *D. lauta*	13.8 - 13.4									

B = barren of diatoms, NA = No age diagnostic diatoms

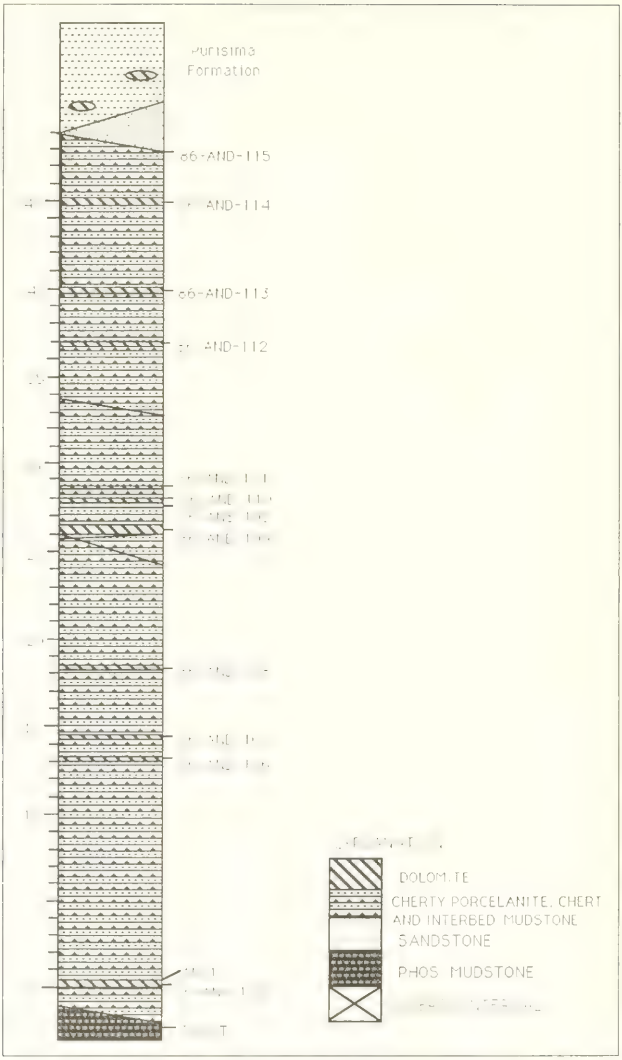


FIGURE 4. Lithostratigraphy of the Monterey Formation at Año Nuevo, located on the northeast limb of the anticline. Scale to the left of the column is in meters; shown to the right of the column is the stratigraphic position of the samples collected.

D. hustedtii and suggest that it is equivalent to the *D. lauta*/*D. hustedtii*-*D. lauta* zone boundary (13.8 Ma). A section dipping to the southwest of the anticline has also been investigated in detail by White (1989) and Omarzai et al. (1990) and it ranges in age from 14.66 Ma at the base to approximately 13.7 Ma at the top. The age of the base of this section (which conformable overlies calcareous mudstones of the lower Monterey Formation) is well constrained by both diatom biostratigraphy and magnetostratigraphy and is probably a more accurate estimate.

Mussel Rock

The Monterey Formation at Mussel Rock is one of the most complete Monterey sections exposed in the Santa Maria basin. A general age estimate of the black chert interval is obtained by dating samples collected from the base and the top of the chert-bearing interval (middle member, Woodring and Bramlette 1950), with additional diatoms dates from the lower and upper members (Fig. 5 and Table 3). Overall, diatoms are few to common and show moderate preservation.

A dolomite concretion collected from phosphatic shales in the lower member of the Monterey Formation (86-MRD-06) yielded diatoms characteristic of *D. hustedtii*-*D. lauta* subzone a, which ranges in age from 13.8–12.7 Ma (White 1989) (Fig. 2). Samples 86-MRD-04 and 87-MRD-26, collected near the base of the middle cherty member of the Monterey Formation, yielded the diatoms *D. praedimorpha* and *D. hustedtii*. The first appearance of *D. praedimorpha* is 12.7 Ma, and therefore the boundary between the lower phosphatic and the cherty middle members of the Monterey Formation probably approximates the boundary between *D. hustedtii*-*D. lauta* subzone a and subzone b and is therefore 12.7 Ma (Fig. 5, Table 3).

Three of the six samples collected across the boundary between the cherty middle member and the porcelaneous upper member were barren or yielded no age diagnostic diatoms (Table 3). Sample 87-MRD-12A(*) yielded only *D. hustedtii*, and it could be in either subzone b or subzone c of *D. hustedtii*-*D. lauta*. Dolomite sample 87-MRD-9A was collected near the top of the last abundant black chert beds. It yielded *Lithodesmium reynoldsii*, whose first appearance coincides with the boundary between *D. hustedtii*-*D. lauta* subzone c and subzone d at an age of 8.9 Ma (Fig. 2). Therefore, the top of the black chert interval is probably around 8.9 Ma but could be as young as 8.2 Ma.

Lions Head

Approximately 70 m of middle member of the Monterey Formation, (Woodring and Bramlette 1950), dominated by fractured black chert and interbedded phosphatic shales, siliceous shales, and dolomite beds, was measured from exposures at Lions Head (Figs. 1, 6). Wornardt (1986), using diatoms recovered from dolomites, estimated the age of the middle Monterey Formation at Lions Head section to be 13.3–11.3 Ma. Dunham and Blake (1987) applied diatom biostratigraphy to chert sequences in their investigation of the Lions Head section and concluded that the middle member correlates to *D. hustedtii*-*D. lauta* subzones a–c, which suggests an age of 13.8–8.9 Ma. The ages resulting from the present work are very close to these two estimates.

Unfortunately, age diagnostic diatoms were recovered from only one-third of the dolomite beds that were sampled. Sample 87-LHD-13 is the stratigraphically lowest dolomite sampled in the middle member, and it yielded only *D. praedimorpha* (Table 4). The next dolomite bed sampled was 87-LHD-14, which lies 2 m above sample 87-LHD-13 (Fig. 6). It yielded a more diverse assemblage and better constrains the age of the base of the section. It contained the following diatoms: *D. hustedtii*, *D. praedimorpha*, *D. lauta*, and

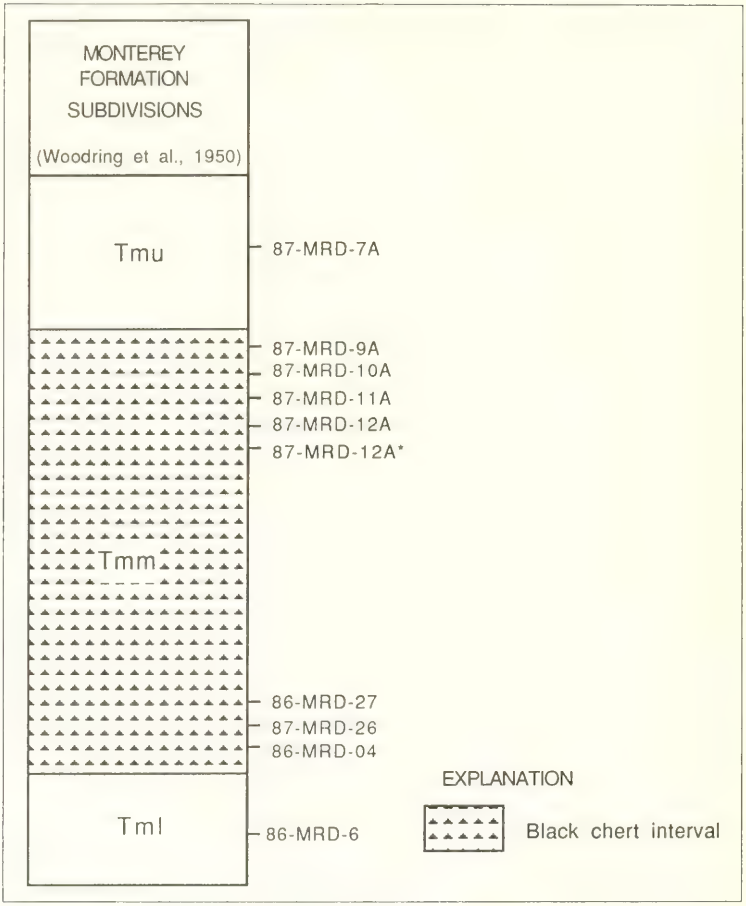


FIGURE 5. Approximate stratigraphic position of samples taken from the Mussel Rock section of the Monterey Formation. Section was not measured in detail, therefore no scale is shown. The subdivisions of the Monterey Formation are after Woodring and Bramlette (1950), where Tml = lower Monterey Formation, Tmm = middle Monterey Formation, and Tmu = upper Monterey Formation.

Rhizosolenia barboi (Table 4). *Rhizosolenia barboi* restricts the lower age limit to 11.4 Ma, which is its first appearance datum and the *D. hustedtii-D. lauta* subzone b/c boundary (Fig. 2). *Denticulopsis praedimorpha*, in the same slide, implies an age older than 10.4 Ma, so sample 87-LHD-14 is likely between 11.4 and 10.5 Ma (Table 4).

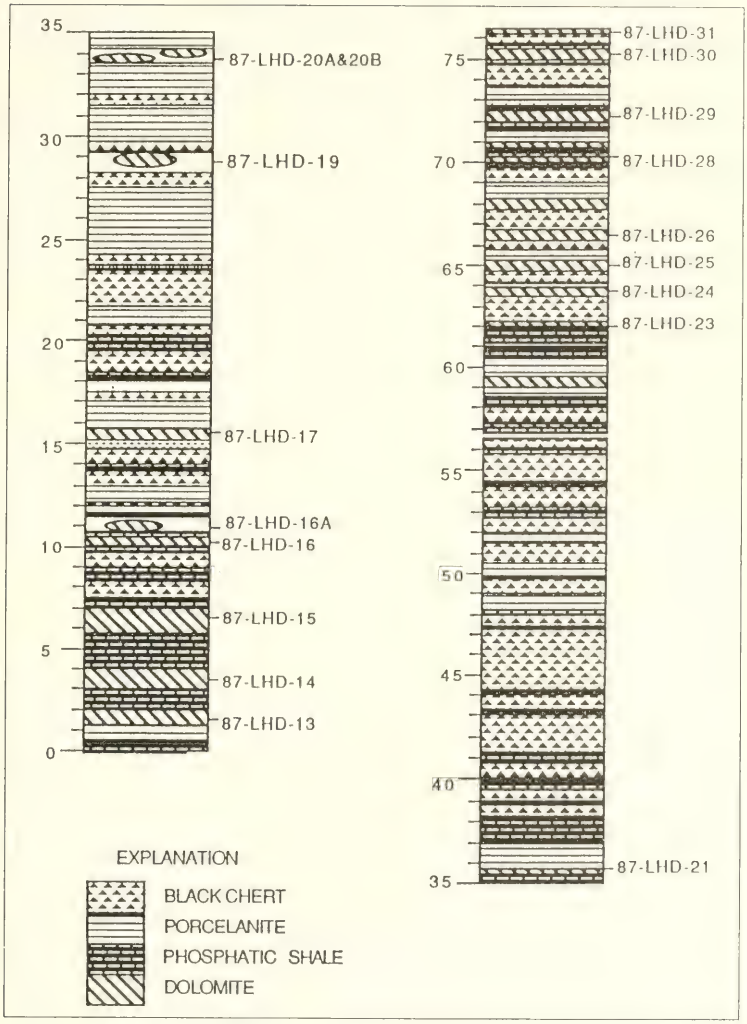


FIGURE 6. Lithostratigraphy of Lions Head section. Scale to the left of the column is in meters; shown to the right of the column is the stratigraphic position of the samples collected

TABLE 4. List of age diagnostic diatoms from the Lions Head section showing zones and stratigraphic interval of samples. Diatom zonation is after Barron (1986a).

Sample	Strat. interval (m)	Diatom zone	Age (Ma)	*Coscinodiscus marginatus*	*Denticulopsis hustedtii*	*D. hyalina*	*D. lauta*	*D. praedimorpha*	*Rhizosolenia barboi*
87-LHD-31	75.01	*D. hustedtii - D. lauta*	B						
87-LHD-30	74.18		B						
87-LHD-29	72.5		B						
87-LHD-28	71.83		B						
87-LHD-26	66.87		B						
87-LHD-25	65.37		B						
87-LHD-24	64.34				X				
87-LHD-23	63.09		B						
87-LHD-21	35.61		B						
87-LHD-20A	33.68	c	>10.4					X	
87-LHD-20B	33.43		B						
87-LHD-19	28.75							X	
87-LHD-17	14.15							X	
87-LHD-16A	10.95		B						
87-LHD-16	10.1		B						
87-LHD-15	6.5		B						
87-LHD-14	3.0			X		X	X	X	X
87-LHD-13	1.0	b	11.4-10.5					X	

B = barren of diatoms

Summary and Conclusions

Chert and porcelanite intervals of the Monterey Formation in coastal Neogene basins have previously lacked reliable age control because of the poor preservation of diatoms in large parts of the sections. Moderately to well-preserved diatoms have been recovered from dolomite beds in these sections, which has allowed the application of diatom biostratigraphy. Precise age control of this interval along the California margin has yielded important insights into its chronostratigraphic distribution.

Cherty intervals in the Bodega and Outer Santa Cruz basins are probably time equivalent and are mostly restricted to the diatom zones *D. lauta* b and the lower part of *D. hustedtii-D. lauta* subzone a. Numerical age estimates for the Pt. Reyes section are roughly 15.0–13.4 Ma and for Año Nuevo section are approximately 14.7–13.7 Ma. The tops of the chert-bearing sections at Pt. Reyes and Año Nuevo are unconformities. The cherty intervals at these two sections were probably thicker, but were erosionally thinned following Miocene sea level falls (Garrison and Ramirez 1989). Erosional events thus removed part of the cherty interval in the on-land sections of the Outer Santa Cruz and Bodega basins, so that the upper age limit of this facies cannot be determined.

Cherty intervals investigated at both Mussel Rock and Lions Head in the Santa Maria basin suggest the ages of the sections are 12.7–8.9 Ma and 11.4–9.2 Ma, respectively.

The next samples to yield age diagnostic diatoms are 87-LHD-17 and 87-LHD-18 at 14.15 m and 28.75 m (Fig. 6, Table 4). They both contained *D. praedimorpha*, which is consistent with *D. hustedtii-D. lauta* subzone c. The last sample to yield *D. praedimorpha* is 87-LHD-20A, 33.7 m above the base of the section; the age of the section at this level is therefore equivalent to or younger than 10.4 Ma (Table 4). The next and last dolomite sample to have preserved diatoms is 87-LHD-24, at 63.3 m above the base of the section, and it contained only *D. hustedtii*, also characteristic of *D. hustedtii-D. lauta* subzone c. Unfortunately, the remaining seven dolomites sampled above 87-LHD-24 are completely barren of diatoms (Table 4). Based on sedimentation rates for the section discussed in White (1989) the top of the section may be as old as 10.3 Ma or as young as 9.2 Ma.southerly Santa Maria basin. The age of the base of the chert-bearing intervals at Pt. Reyes and Pt. Año Nuevo is 2 my older than the age of the base of cherty intervals of the Monterey Formation at Mussel Rock and Lions Head (White 1989, 1990). This stratigraphic distribution indicates that sedimentation of the precursor material to the cherts in the Bodega and Outer Santa Cruz basins occurred about 2 million years earlier than in the Santa Maria Basin. The cause of the diachronous distribution pattern is probably related to varying latitudinal effects of cooling global temperature and increasing circulation during the early Middle Miocene (White 1989, 1990).

Acknowledgements

This manuscript summarizes data from the author's dissertation that was conducted at the University of California at Santa Cruz under the supervision of R. E. Garrison. Invaluable assistance during the course of the investigation was also provided by J. A. Barron of the U. S. Geological Survey. Reviews by E. Fourtanier and P. Kociolek are gratefully appreciated.

Literature Cited

BAKER, P. A. AND M. KASTNER. 1981. Constraints on the formation of sedimentary dolomite. Science 213:215–216.

BARRON, J. A. 1986a. Updated diatom biostratigraphy for the Monterey Formation of California. *In* Siliceous microfossil and microplankton studies of the Monterey Formation and modern analogs, R. E. Casey and J. Barron, eds. Pac. Sec. S. E. P. M. 45:105–119.

———. 1986b. Paleoceanographic and tectonic controls on deposition of the Monterey Formation and related siliceous rocks in California. Palaeogeogr. Palaeoclimat. Palaeoecol. 53:27–45.

CLARK, J. C. 1981. Stratigraphy, paleontology and geology of the central Santa Cruz Mountains, California Coast Ranges. U. S. Geol. Surv. Prof. Pap. 1168:1–51.

DUNHAM, J. B. AND G. H. BLAKE. 1987. Guide to the coastal outcrops of the Monterey Formation of western Santa Barbara County, California. *In* Guide to the coastal outcrops of the Monterey Formation of western Santa Barbara County, California, J. B. Dunham, ed. Pac. Sec. S. E. P. M. 53:1–36.

GARRISON, R. E. AND P. C. RAMIREZ. 1989. Conglomerates and breccias in the Monterey Formation and related units as reflections of basin margin history. *In* Conglomerates in Basin Analysis: A Symposium Dedicated to A. Woodford. I. Colburn and P. Abbott, eds. Pac. Sec. S. E. P. M. 62:189–206.

KASTNER, M., K. A. MERTZ, D. HOLLANDER, AND R. E. GARRISON. 1984. The association of dolomitite-phosphorite-chert: causes and possible diagenetic sequences. *In*

Dolomites of the Monterey Formation and other organic-rich units, R. E. Garrison et. al., eds. Pac. Sec. S. E. P. M. 41:75–86.

LAGLE, C. W. 1984. Recovery of siliceous microfossils by disaggregation of dolomite. *In* Dolomites of the Monterey Formation and other organic-rich units, R. E. Garrison et. al., eds. Pac. Sec. S. E. P. M. 41:185–194.

MACKINNON, T. C. 1989. Petroleum geology of the Monterey Formation in the Santa Maria and Santa Barbara coastal and offshore areas. Pp. 11-27 *in* Oil in the California Monterey Formation, Field Trip Guidebook T311. 28th Intern. Congr.

OMARZAI, S. K., R. COE, AND J. BARRON. 1990. Magnetic polarity stratigraphy of the Miocene Monterey Formation of California at Point Año Nuevo, Outer Santa Cruz Basin. EOS Trans. Am. Geophys. Union 71:1285.

PISCIOTTO, K. A. AND R. E. GARRISON. 1981. Lithofacies and depositional environments of the Monterey Formation, California. Pp. 97-122 *in* The Monterey Formation and related siliceous rocks of California, R. L. Garrison et. al., eds. Pac. Sec. S. E. P. M. Special Publication.

REDWINE, L. E. 1981. Hypothesis combining dilation, natural hydraulic fracturing, petroleum expulsion and dolomitization to explain petroleum reservoirs in Monterey Shale, Santa Maria area, California. Pp. 221-248 *in* The Monterey Formation and related siliceous rocks of California, R. L. Garrison et. al., eds. Pac. Sec. S. E. P. M. Special Publication.

ROEHL, P. O. 1981. Dilation brecciation—a proposed mechanism of fracturing, petroleum expulsion and dolomitization in the Monterey Formation, California. Pp. 285–316 *in* The Monterey Formation and related siliceous rocks of California, R. L. Garrison et. al., eds. Pac. Sec. S. E. P. M. Special Publication.

WHITE, L. D. 1989. Chronostratigraphic and paleoceanographic aspects of selected chert intervals in the Miocene Monterey Formation, California. Ph.D. dissertation, University of California, Santa Cruz. 236 p.

———. 1990. Stratigraphy and paleoceanographic history of the Monterey Formation at Pt. Reyes and Pt. Año Nuevo, California. Pp. 91–104 *in* Geology and Tectonics of the Central California Coast Region, San Francisco to Monterey, R. L. Garrison et. al., eds. Volume and Guidebook GB67.

WOODRING, W. P. AND M. N. BRAMLETTE. 1950. Geology and paleontology of the Santa Maria district, California. U. S. Geol. Surv. Prof. Pap. 222:1–142.

WORNARDT, W. W., Jr. 1986. Diatom biostratigraphy from diatomaceous dolomites and shales in the Monterey Formation, Rodeo Canyon, Pt. Pedernales and Lions Head sections, southwestern Santa Barbara County, California. *In* Siliceous microfossil and microplankton studies of the Monterey Formation and modern analogs, R. E. Casey and J. A. Barron, eds. Pac. Sec. S. E. P. M. 45:141–147.

Dynamics of Epiphytic Diatoms on *Cladophora glomerata* in the Tvärminne Archipelago, Northern Baltic Sea

by

Elina Leskinen and Guy Hällfors

University of Helsinki, Department of Botany,
Hydrobiological Laboratories, Fabianinkatu 24 A,
00100 Helsinki, Finland

with 3 figures and 2 tables

Abstract: Seasonal changes in the structure of a diatom community were studied in relation to the age of the substrate and to several environmental parameters. Diatoms growing on *Cladophora glomerata* were sampled ten times during the growing season of 1979 in the outer, unpolluted, brackish-water archipelago at Tvärminne, southwestern coast of Finland. Numbers of diatom valves varied between 23 and 5500 per µg sample (dry weight), being smallest in samples from early summer and early winter. The number of species in the samples varied between 8 and 35, and appeared to increase with the age of the substrate. The lowest number of species, however, was found in samples with the highest epiphyte biomass in late August.

Dominance was high in early summer on young *Cladophora*, which formed two belts in the hydrolittoral. During the height of the summer, dominance gradually decreased with the increasing age of the substrate. The dominant species were *Diatoma elongatum* and *Rhoicosphenia abbreviata*, which frequently exceeded 50 % of the counts. At the end of August a new *Cladophora* belt developed at a higher level. With rapidly falling water temperature, further development was slow and the difference between the belts persisted until the end of the growing season.

Canonical correspondence analysis (CCA) showed a circular arrangement of successive sampling occasions, indicating strong seasonality in species composition. The summer communities were mainly influenced by light and temperature. In the beginning of summer, *D. elongatum*, a common species of all seasons, dominated in all samples. In late summer and autumn the communities responded mainly to increasing nutrient concentrations and decreasing light. At the end of the summer characteristic species were *Opephora olsenii* and *Epithemia* spp., whereas in autumn *Licmophora* spp. became most prominent.

Introduction

The northern Baltic Sea and the Gulf of Finland especially are rapidly being eutrophicated (Wulff et al. 1986; Elmgren 1989). Therefore, information on community structure of the resident biota in areas little affected by eutrophication is urgently needed. The present

contribution examines material collected before the latest acceleration in environmental deterioration, vis-à-vis the diatoms epiphytic on *Cladophora glomerata*. *Cladophora glomerata* appears to be a very useful species to sample for epiphytic diatom assemblages since sampling is simple and the samples are easily processed into relatively clean diatom preparations. Being essentially a hydrolittoral plant, *C. glomerata* is also widely distributed, so that it can be found practically everywhere in the Baltic Sea from early June until late autumn.

There are few previous investigations of diatom:substrate relationships from this area. Rautiainen and Ravanko (1972) described the epiphytic diatom flora of macrophytes, including *C. glomerata*, in the southwestern archipelago of Finland, but a detailed community analysis was not included. Rönnberg and Lax (1980) studied the effect of wave action on the epiphytic diatoms of *C. glomerata*, but again without powerful statistical methods. Leskinen and Hällfors (1990) applied ordination (DCA) to describe the effects of eutrophication on diatom communities epiphytic on *C. glomerata* at the south coast of Finland. Snoeijs (1988) provided a checklist of epilithic and epiphytic diatoms from Forsmark, Sweden, without specifying the substrates of the epiphytes. Hällfors and Niemi (1989) listed the epiphytic diatoms in a small number of samples, two of which were of *C. glomerata*, from a small island at the south coast of Finland.

In the present study we have analyzed seasonal changes in the structure of the diatom community epiphytic on *C. glomerata* in relation to the age of the substrate and environmental parameters at different depths in the hydrolittoral during one complete growing season in 1979. The power of Canoco (ter Braak 1987) has been successfully applied to epilithic diatom assemblages by Snoeijs (1989), and it was used for ordination in the present study. Community structure, dominance, and evenness are illustrated by graphic presentation based on the log normal distribution, similar to K-dominance curves (Leskinen and Sarvala 1988).

Materials and Methods

The sampling locality, Kvarnskärsgrundet, lies in the Tvärminne archipelago southwest of the Hanko peninsula in the Baltic Sea (salinity ca. 6 ‰), close to Tvärminne Zoological Station (Fig. 1). The sampling site was an east-northeast-facing slope on a moderately exposed rocky shore. The diatoms on *C. glomerata* were sampled ten times during its the growing season. Sampling was limited to the hydrolittoral belt, which reaches down to about 0.7 m below mean water level in the area. Care was taken not to disturb the epiphytes attached to the filamentous algal substrate. Therefore samples were gently detached with forceps by a diver and put into sample jars underwater.

Hydrographical and hydrochemical factors, salinity, temperature, chlorophyll *a* concentration, and ammonium, nitrate, phosphate and silicate concentrations were measured at a sampling site 1 km from the sampling station where diatom samples were collected (Hällfors et al. 1983). These environmental data were used as passive factors for the canonical correlation analysis that was applied to the species data.

In the laboratory algae were filtered onto preweighed cellulose filters (Schleicher and Schüll no. 1575) and dried (70°C, 24 h) to determine dry weight. The organic matter was then oxidized by boiling the filters with the algae in concentrated nitric acid followed by an addition of concentrated sulfuric acid. After washing by centrifugation with at least five changes of distilled water, the samples were diluted to a known volume. Slides for microscopic examination were prepared by pipetting 50 µl of the oxidized sample suspension onto a cover glass, which was allowed to dry under a hood, and then mounted in

Clophenharpiks. Diatoms were identified and counted with a Leitz Dialux microscope fitted with a 100× planapochromatic phase-contrast oil immersion objective (N. A. 1.32). The number of valves counted per sample varied from 859 to 1613 (Table 1).

The distribution of the relative abundances of the species was examined with K-dominance curves (Lambshead *et al.* 1983). Canonical correspondence analysis with log-transformation and downweighing of rare species (ter Braak 1987) was used to examine similarities or differences between the sampling sites that could be attributed to external factors (the program Canoco).

Results and Discussion

Phenology of *Cladophora Glomerata*

Ice scouring during the winter and periods of low sea level in spring usually eliminate *C. glomerata* from the upper two-thirds of the hydrolittoral belt. When algal growth starts in spring after the melting of the ice, *Pilayella littoralis* occupies the available bare rock. Only in June, when water temperature reaches about 10°C, does *C. glomerata* start to grow from overwintering basal remains, forming a first belt in the lower part of the hydrolittoral. Meanwhile, as *Pilayella* gradually decreases, and as the water level rises, new substratum becomes available. In July a second belt of *C. glomerata* is usually formed by zoospores from plants in the first belt, some 0.1–0.2 m higher in the hydrolittoral. If the sea level has continued to rise in August, a third generation may form a belt above the first two.

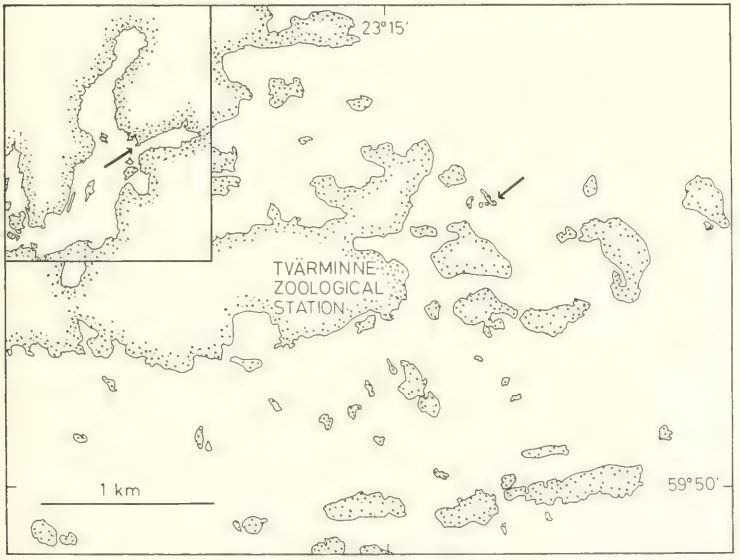


FIGURE 1. Location of the sampling site in the Tvärminne archipelago, Northern Baltic.

TABLE 1. Diatom species observed and their occurrence on *Cladophora glomerata* in different seasons at Kvarnskärsgrundet, Tvärminne. BS = beginning of the summer (June 15 and July 4); MS = middle of the summer (July 24 and August 2); ES = end of the summer (August 31 and September 20); A = autumn (October 2 and 25); BW = beginning of the winter (November 17 and December 19); - = taxa not found in the samples; + = taxa found in at least one of the samples; ++ = abundance 5 %; and +++ = abundance 10 % in at least one of the samples.

	BS	MS	ES	A	BW
EUPODISCALES					
Cyclotella caspia Grunow	-	+	+	+	+
Melosira lineata (Dillwyn) Agardh	+	+	+	+	-
M. nummuloides (Dillwyn) C.A. Agardh	-	-	-	+	-
Skeletonema costatum (Greville) Cleve	+	+	++	+	+
Thalassiosira weissflogii (Grun.) Fryxell & Hasle	+	+	-	+	-
T. spp.	+	+	+	+	+
BACILLARIALES					
Achnanthes biasolettiana (Kützing) Grunow	-	+	-	-	-
A. delicatula (Kützing) Grunow	+	+	+	-	+
A. lemmermannii Hustedt	+	-	-	-	-
A. taeniata Grunow	+	-	+	-	+
A. sp. 1	+	+	+	+	+
Amphipleura rutilans (Trentepohl) Cleve	+	+	+	+++	++
Amphora coffeaeformis Agardh	+	+	-	-	-
A. delicatissima Krasske	+	+	+	-	-
A. spp.	-	++	-	-	-
Bacillaria paxillifer (Müller) Hendey	-	-	-	+	-
Cocconeis pediculus Ehrenberg	+	+	+	+	++
C. peltoides Hustedt	-	+	-	-	-
C. placentula Ehrenberg	+	-	-	+	-
C. scutellum Ehrenberg	-	+	-	+	-
Diatoma elongatum (Lyngbye) Agardh	+++	+++	+++	+++	+++
D. vulgare Bory	+	-	-	-	-
Entomoneis sp. 1	-	+	-	-	-
Epithemia sorex Kützing	-	+	+	-	-
E. turgida (Ehrenberg) Kützing	+	++	+	-	-
E. zebra (Ehrenberg) Kützing	-	+	-	-	-
Fragilaria construens (Ehrenberg) Grunow	-	+	-	-	-
F. hyalina (Kützing) Grunow	-	+	++	++	+
F. intermedia Grunow	+	+	-	+	-
F. mutabilis (W.Smith) Grunow	+	+	+	+	+
F. pinnata Ehrenberg	+	+	-	-	-
Gomphonema exiguum Kützing	+	+++	+++	++	+
G. olivaceum (Lyngbye) Kützing	+	+	+	+	+
G. pseudexiguum Simonsen	-	-	+	-	-

TABLE 1, continued.

	BS	MS	ES	A	BW
Licmophora communis (Heiberg) Grunow	-	-	+	+	+
L. debilis (Kützing) Grunow	-	+	+	++	+
L. gracilis (Ehrenberg) Grunow	+	+	+	+++	++
L. cf. *oedipus* (Kützing) Grunow	-	-	-	-	+
Navicula cari v. *recens* Lange-Bertalot	-	-	-	-	+
N. cryptocephala Kützing	-	-	-	-	+
N. gregaria Donkin	-	+	-	+	-
N. hansenii M.Möller	+++	++	+	+++	+++
N. kepesii Grunow	-	-	+	-	-
N. salinarum Grunow	+	-	-	-	-
N. cf. *strenzkei* Hustedt	+	-	-	-	-
N. tripunctata (O.F. Müller) Bory	+	-	-	+	-
N. veneta Kützing	+	+	+	-	+
N. sp. 1	+	-	-	-	-
N. sp. 6	-	+	+	-	-
N. sp. 7	-	+	+	-	-
N. spp.	+	-	-	-	-
Nitzschia communis Rabenhorst	-	+	-	+	-
N. frustulum (Kützing) Rabenhorst	+	+++	+	+	-
N. gandersheimiensis Krasske	-	+	-	-	-
N. microcephala Grunow	+	+	+	+	-
N. palea (Kützing) W.Smith	+	-	-	-	-
N. paleacea Grunow	+	+	+	+	+
N. cf. *pseudonana* Hasle	-	-	-	+	-
N. romana Grunow	+++	+	+	+	+
N. valdestriata Aleem & Hustedt	+	+	-	-	-
N. spp.	-	+	+	+	+
Opephora olsenii M. Möller	+	+	-	-	-
Pleurosigma salinarum Grunow	+	-	-	-	-
Rhoicosphenia abbreviata (C. Ag.) Lange-Bertalot	+	+++	+++	+++	+++
Rhopalodia gibba (Ehrenberg) O.Müller	-	+	-	-	-
Synedra barbatula Kützing	+	+++	+	+	+
S. pulchella (Ralfs) Kützing	+	+	+	+	+
S. tabulata (C. Agardh) Kützing	+	+++	+++	+++	+
Number of diatom species (total 68):	42	48	36	35	28
Number of diatom species specific to one season (total 25):	9	7	2	3	3

Soon after mid-July *Idotea baltica* regularly releases its brood (Salemaa 1979), and the young start to feed on *C. glomerata* and its epiphytes (Jansson 1967, 1974). In August *Cladophora* tufts usually become reduced to main axes and a few clusters of apical branches.

DIATOM SPECIES

A total of 68 diatom species were observed in the material. Species occurring at all sampling times were common littoral types, most of which attach to surfaces with a

mucilaginous pad or tube. These include: *Amphipleura rutilans*, *Cocconeis pediculus*, *Diatoma elongatum*, *Fragilaria mutabilis*, *Gomphonema exiguum*, *G. olivaceum*, *Licmophora gracilis*, *Navicula hansenii*, *Nitzschia paleacea*, *N. romana*, *Rhoicosphenia abbreviata*, *Synedra barbatula*, *S. pulchella*, and *S. tabulata* (Table 1). The highest number of species in a sample was 35, found on a *Cladophora* stand a few weeks old, and the lowest number of species in any one sample was eight, on a newly developed *C. glomerata* thallus (Table 2).

The number of species in a sample generally increased with the age of the substrate and, therefore, the age of the periphytic assemblage. Sea level rises irregularly throughout the summer in the study area (Hällfors et al. 1983; Hällfors 1984), and successive belts of filamentous algae tend to grow at different levels, with the youngest belts closest to the surface. The lowest number of species, nine at August 31 and eight at September 20, were found on these young thalli. The same observation was made also in the inner archipelago (Leskinen and Hällfors 1990). The highest number of species was found in the middle of summer, in late July to beginning of August, in the oldest *Cladophora* belt, before it had been grazed down by the newly hatched generation of *Idotea baltica*.

TABLE 2. Östra Kvarnskärsgrundet. The number of diatom species, the density of diatoms (number of valves per dry weight [µg] of *Cladophora glomerata*), and the number of valves counted per sample.

Date	Depth (m)	Depth from surface(m)	Species nr.	Valves /µg host dry wt.	Valves counted /sample
15.06.1979	0.4	0.1	31	174.4	1131
	0.7	0.4	29	202.6	1046
04.07.1979	0.7	0.7	30	287.8	1036
24.07.1979	0.3	0.6	25	551.1	1000
	0.7	1.0	25	777.7	1317
02.08.1979	0.7	0.6	35	120.3	910
	0.7	0.6	27	120.0	1426
	0.9	0.8	30	138.6	859
31.08.1979	0.2	0.1	9	5474.2	1045
	0.6	0.5	14	2928.8	1278
	0.9	0.8	16	2711.6	1019
	0.9	0.8	25	2183.7	1003
20.09.1979	0.6	0.3	8	1269.0	1033
	0.7	0.4	16	2216.9	1613
	0.9	0.6	21	602.6	1093
02.10.1979	0.1	0.1	15	1232.4	1098
	0.4	0.4	23	443.5	1006
	0.6	0.6	23	588.7	1119
25.10.1979	0.1	0.0	13	1262.8	1056
	0.5	0.4	20	909.3	1140
	0.8	0.7	24	595.0	1151
17.11.1979	0.1	0.1	16	27.4	1114
	0.3	0.3	17	214.3	1009
	0.5	0.5	17	288.8	1122
19.12.1979	0.5	0.5	17	23.4	1074

Valves from living and dead diatoms could not be separated. *Achnanthes taeniata*, *Cyclotella caspia*, *Skeletonema costatum*, and *Thalassiosira weissflogii* do not normally form littoral populations. Their occurrence in our samples is regarded as fortuitous. Examination of living material indicates that the number of dead valves was insignificant in the hydrolittoral belt in late summer.

Diatom Density

Diatom density varied from 23–5474 valves per µg sample dry weight (Table 2). Density was greatest in August and September, when the diatom communities were relatively old and mature, the nutrient concentration in the water was rather high, and there was still enough light for diatom growth. Diatoms are limited in the early summer by the low nutrient level, in late summer by grazing, and in autumn by light.

Around midsummer (June 15 and July 24) the diatom density was lowest near the surface. This may be an indication of light inhibition, as the weather was rather calm in that period (Hällfors et al. 1983) and wave action could hardly detach diatoms in significant numbers. Later in summer and in autumn, densities were higher near the surface where light intensity was strongest, except September 20 and November 17, when storms had reduced the number of valves particularly near the surface.

Community Structure and Dominance

Dominance was high in the early summer on the young *Cladophora*, which formed two belts in the hydrolittoral. The dominant species was *Diatoma elongatum*. Towards the end of the summer dominance gradually decreased with increasing substrate age, and the most common species were *Rhoicospenia curvata* and *Gomphonema exiguum* (Fig. 2). At the end of August the weather deteriorated, the water level rose, and a new *Cladophora* belt developed at a higher level. The most abundant diatom species on the new *Cladophora* was again *Diatoma elongatum*, which represented 80 % of the community. The dominance of *Rhoicospenia curvata* persisted on the older *Cladophora* belt. With rapidly falling water temperature and diminishing light, further development was slow and the difference between the three belts persisted until the end of the growing season.

Seasonal Change in Community Structure

Canonical correlation analysis produced two dominant ordination axes with eigenvalues 0.23 and 0.12 (the two other axes analyzed had eigenvalues 0.08 and 0.06). The circular arrangement of successive sampling occasions in the analysis indicated strong seasonality in species composition (Fig. 3). Differences between community structure of successive samplings appeared greater during the summer months than during the autumn, when the canonical correlation analysis grouped samples closer together. The most important environmental factors affecting the diatoms were nutrients, especially nitrate and phosphate. Silicate was of less importance, and the effect of ammonium was not significant according to the analysis. Of the other environmental factors, light intensity was the most significant, then water temperature, and depth of the sampling site. The effect of salinity was negligible. The amount of chlorophyll in the surrounding water was also tested as an environmental variable, but it was found to be nonsignificant.

In the beginning of the summer, *Diatoma elongatum*, a common species at all seasons, was strongly dominating in all samples. Other characteristic species were *Achnanthes taeniata*, *Fragilaria pinnata*, *Amphora coffaeiformis*, and *Navicula veneta*. Environmental factors most influential at this time of the year were high light intensities and the lack of nutrients. In the middle of the summer, diatom communities responded both to high light intensity and water temperature. Characteristic species for these communities were *Opephora olsenii*, *Epithemia sorex*, *E. turgida*, and *E. zebra*. *Melosira nummuloides*, *Lic-*

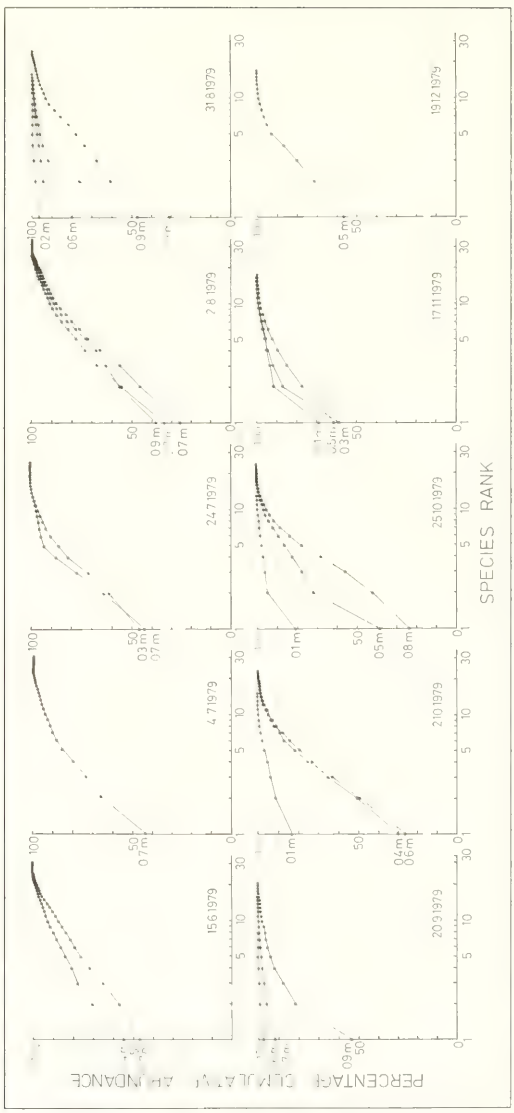


FIGURE 2. K-dominance curves for samples from different sampling depths taken 10 times during the growth period of *Cladophora glomerata* in 1979.

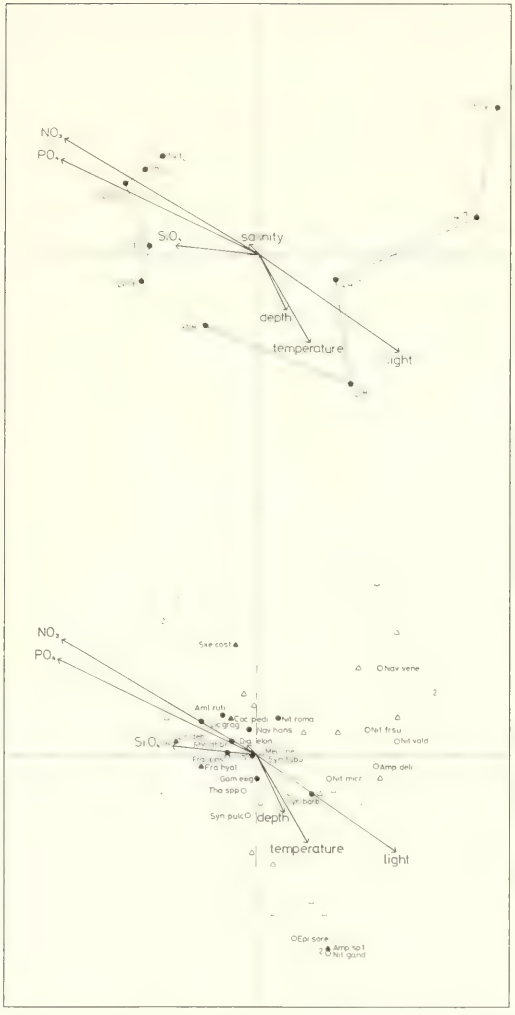


FIGURE 3. Ordination for (a) centroids of sampling dates and (b) species scores showing the first (vertical) and the second axes (horizontal) of canonical correspondence analysis. Species scores: closed circle = 10 %, closed triangle = 5 %, open circle = 1 % abundance in at least one of the samples, and open traingle = < 1 % in all the samples. The arrows show the direction of variation in the environmental factors.

mophora communis, and *L. debilis* characterized the autumn communities. In the early winter common species that were otherwise rare included *L.* cf. *oedipus* and *Navicula cryptocephala*.

At the end of the summer the most important environmental factor influencing the diatoms was silicate, later in the autumn phosphate, nitrate, and ammonium were important, and in the beginning of the winter an important vector was the high salinity of the water. The effect of salinity was, however, probably not as great as that of the nutrients and the lack of light.

Successional Observations

Diatoma elongatum is the main pioneering species on *Cladophora glomerata*. It is present both in the plankton and benthos throughout the growing season. As an epiphyte, it produces zigzag chains from which single cells or short chains easily break away to colonize available surfaces or continue growth in the pelagic zone. The pelagic zone provides a pool of cells for long-distance dispersal. *Diatoma elongatum* is also an opportunistic species favored by low water temperatures and high nutrient concentrations. It is abundant in plankton in the late stages of the vernal bloom (Niemi 1973), before *C. glomerata* starts to grow. In summer, it is greatly favored by upwelling events, characterized by falling surface temperatures and increased nutrient levels, when *Diatoma elongatum* usually colonizes all available substrates in the hydrolittoral and lower geolittoral zones (Hällfors and Niemi 1989).

Subsequent colonizers have smaller pelagic populations than *D. elongatum* to serve as inocula. *Cocconeis pediculus* arrives early, favoring young parts of *Cladophora* thalli. The cells are remarkably well adapted to epiphytism on *Cladophora*, as the transapical axis exhibits the same curvature as *Cladophora* cells. *Licmophora* species, especially *L. gracilis*, seem to favor relatively young *Cladophora* as well; their development may be enhanced by upwelling. On somewhat older parts of *Cladophora*, *Synedra* spp., *Rhoicosphenia abbreviata*, *Fragilaria hyalina*, and *Gomphonema* spp. are usually dominant, while the oldest, basal parts are dominated by *Epithemia* spp. and *Nitzschia* spp.

Acknowledgements

The investigation was financially supported by the Walter and Andrée de Nottbeck Foundation, the Maj and Tor Nessling Foundation, the University of Helsinki, and the Academy of Finland. Tvärminne Zoological Station provided excellent working facilities.

Literature Cited

Elmgren, R. (1989). The eutrophication status of the Baltic Sea: Input of nitrogen and phosphorus, their availability for plant production, and some management implications. Baltic Marine Environment Protection Commission, Second Seminar on Wastewater Treatment in Urban Areas, Visby, Sweden, 6–8 September 1987. Baltic Sea Environ. Proc. 30:12–31.

Hällfors, G., E. Leskinen, and Å. Niemi. 1983. Hydrography, Chlorophyll *a* and nutrients at Tvärminne Storfjärd, Gulf of Finland, in 1979/1980. Sci. Rept. Walter and Andrée de Nottbeck Found. 4:1–19.

Hällfors, G. and Å. Niemi. 1989. Den marina vattenvegetationen vid Gloholmen. Nordenskiöld-Samfundets Tidskrift 48:3–21.

Jansson, A.-M. 1967. The food-web of the *Cladophora*-belt fauna. Helgoländer wissenschaftliche Meeresuntersuchungen 15:574–588.

———. 1974. Community structure, modelling and simulation of the *Cladophora* ecosystem in the Baltic Sea. Contributions from the Askö Laboratory, University of Stockholm, Sweden, No. 5. 130 pp.

LAMBSHEAD, P. J. D., H. M. PLATT, AND K. M. SHAW. 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. J. Nat. Hist. 17:859–874.

LESKINEN, E. AND G. HALLFORS. 1990. Community structure of epiphytic diatoms in relation to eutrophication by the Hanko peninsula, S. coast of Finland. Pp. 323–333 *in* Proc. 10th Int. Diatom Symp., H. Simola, ed. Koeltz Scientific Books, Koenigstein.

LESKINEN, E. AND J. SARVALA. 1988. Community analysis of diatom colonization on artificial substrata in a northern Baltic Sea archipelago: A comparison of methods. Ann. Bot. Fenn. 25:21–32.

NIEMI, Å. 1973. Ecology of phytoplankton in the Tvärminne area, SW coast of Finland. I. Dynamisces of hydrography, nutrients, chlorophyll *a* and phytoplankton. Acta Bot. Fenn. 100:1–68.

RAUTIANEN, H. AND O. RAVANKO. 1972. The epiphytic diatom flora of the benthic macrophyte communities on rocky shores in the southwestern archipelago of Finland, Seili islands. Nova Hedwigia 22:827–842.

RÖNNBERG, O. AND P.-E. LAX. 1980. Influence of wave action on morphology and epiphytic diatoms of *Cladophora glomerata* (L.) Kütz. Ophelia, Suppl. 1:209–218.

SALEMAA, H. 1979. Ecology of *Idotea* spp. (Isopoda) in the northern Baltic. Ophelia 18:133–150.

SNOEIJS, P. 1988. Ecological studies of epilithic algae and fauna in the Baltic hydrolittoral. Ph.D. thesis, Uppsala University.

SNOEIJS, P. 1989. A check-list of the benthic diatoms at Forsmark (northern Baltic Sea). 1. Epilithic and epiphytic taxa. Ann. Bot. Fenn. 26:427–439.

TER BRAAK, C. J. F. 1987. Canoco—a Fortran program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1) ITI-TNO, Wageningen. 95 pp.

WULFF, F., G. ÄRTEJERG, G. NICOLAUS, Å. NIEMI, P. CISZEWSKI, S. SCHULZ, AND W. KAISER. 1986. The changing pelagic ecosystem of the Baltic Sea. Ophelia, Suppl. 4:299–319.

Planktonic Marine Diatom Winter Stages: Antarctic Alternatives to Resting Spores

by

Greta A. Fryxell

Department of Oceanography, Texas A & M University,
College Station, Texas 77843-3146

with 1 table and 2 plates

Abstract: The planktonic material collected in the austral spring, autumn, and winter from the Weddell/Scotia Sea ice edge on National Science Foundation projects, and during the austral summer both from the plankton and the sediment on a transect south across the Antarctic Circumpolar Current into Prydz Bay on Ocean Drilling Program Leg 119, allowed comparisons between seasons and between living and sediment samples. *Thalassiosira* species are abundant in the austral spring in Antarctic waters, when lightly silicified vegetative stages produce long chains. However, those that are preserved in the sediment have heavily silicified valves and thus contrast with the spring stages. Some heavily silicified valves have been confirmed to be resting spores. However, heavily silicified valves of some species were products of a winter growth stage. During the winter, these cells were even found from 150–200 m depth in the water column, deeply pigmented, and packed with storage products. Particularly evident in the sediment in Prydz Bay, Antarctica, were the heavily silicified valves of *T. ritscheri* (Hustedt) Hasle, nearly linear in areolar pattern, and *T. gracilis* (Karsten) Hustedt, with the central areolae more widely spaced on the thickened winter valves. The heavily silicified winter valves, like the specialized winter growth stage with distinctive morphology of *Eucampia*, appear to be an oceanic alternative to the production of resting spores. Thus, when light is limiting, sporadic growth is possible for these species without the loss of one cell division or thecae. This immediate response by some species to dynamic growth conditions gives an evolutionary advantage at the ice edge and leaves a record of winter growth in the sediment.

Introduction

Antarctic diatoms are known for polymorphism (e.g., Hasle et al. 1971; Fryxell 1977), and opportunities to take part in recent cruises in all four seasons have permitted observations of different life stages. Although resting spores are produced in only a few cases, seasonal environmental conditions influence the expression of morphology in the siliceous frustules of diatoms in Antarctic waters (Fryxell 1989).

It is known that environmental conditions can influence morphology in diatoms from non-polar brackish and marine areas. Changes in salinity cause morphological differences in several species that are not closely related, according to Karayeva and Dzhafarova (1988). With different salinities, Li and Chiang (1979) saw morphological differences in the elevations of *Proteucylindrus* in Taiwan, and Paasche et al. (1975) reported on changes in process lengths in cultures of *Skeletonema*. Differences in degrees of silicification and

accompanying morphological changes were seen as the result of large salinity changes in *Cyclotella cryptica* Reimann, Lewin, & Guillard (Schultz 1971).

Williams (1964), working with motile salt marsh diatoms, found that large changes in salinity could affect division rates. He found maximum division rates at salinities close to 20, although there was good growth for all species at least from salinities of 10–30. Although Antarctic diatoms in the immediate vicinity of ice formation and ice melting could certainly experience such fluctuation, change in salinity probably is not a major factor in growth rates within the water column where smaller changes are seen (austral spring, 34.0–34.5, Nelson et al. 1987; austral winter, 33.9–34.6, Husby et al. 1989). Division rates may also be related to the changes in morphology, and division rates change with the season.

Temperature is related to growth rates and thus to seasonal changes in the field (Eppley 1972, 1977). Even natural cryophilic populations with many species that do not survive at much over 8° C in culture had a maximum rate of photosynthesis at 7° C (Neori and Holm-Hansen 1982). Paasche (1980) found that laboratory data on the effect of temperature on the production of thinner summer forms inconclusive, but he cited Hart's (1942) field statistical data that weakly silicified forms were better correlated with a lowering in silicate concentrations than with increases in temperature. However, Fryxell (1988) used the number of fascicles of areolae on a valve as a morphological indicator of degree of silicification of *Thalassiosira tumida* (Janisch) Hasle in culture, and results indicated that even a small change in temperature was an important factor in degree of silicification. These laboratory results suggested that polymorphic forms were responding in part to realistic seasonal changes in temperature, an idea that could be tested in the field.

Three different kinds of heavily silicified overwintering forms are suggested here as parallel evolutionary winter survival strategies: resting spores, distinctive winter growth stages, and cold water stages. Of these, only the resting spores are not vegetative stages, in that they must germinate before normal vegetative division. All of these can be found in the sediment (with samples that are averaged over time), but their nature is easier to discover when they are noted from living material in the plankton (with samples from a much smaller time/space scale). Since these three heavily silicified stages can be better preserved in the sediments than lightly silicified vegetative stages and thus be even better represented from the sediments than in the water column, their recognition provides both geological and biological insights. Distinguishing features will be described, and specific examples of newly recognized cold water stages will be provided within the genus *Thalassiosira*. Additional examples will be cited from other sources.

Materials and Methods

Participation as a biologist on board the drill ship JOIDES Resolution, on the Ocean Drilling Program Leg 119, December 1987–February 1988, allowed comparison of the phytoplankton on a transect south from the northern Kerguelen Plateau in the southern Indian Ocean into Prydz Bay, Antarctica, during a brief ice-free season (Barron and Larsen et al. 1989). As the five holes in Prydz Bay were drilled, opening-and-closing 35 µm mesh net hauls were made in the water column within a mile of the drill ship from the service vessel, Maersk Master (Kang 1989; Kang and Fryxell 1991). In addition, reference samples have been used from the N. S. F. Program, Antarctic Marine Ecosystem Research at the Ice Edge Zone (AMERIEZ), as summarized in Fryxell and Prasad (1990) and from Antarctic collections in the Weddell Sea made by S. Z. El-Sayed.

Samples were studied alive on board ship and treated as in Simonsen (1974) and Hasle and Fryxell (1970) for shore-based light microscope investigations from permanent mounts.

Observations

Thalassiosira ritscheri (Hustedt) Hasle was described as *Coscinodiscus ritscheri* by Hustedt (1958, p. 117), found only in the Antarctic, and transferred to *Thalassiosira* by Hasle (1968, p. 196). Each strutted process in the central cluster takes the place of an areola (Hasle and Heimdal 1970: Figs. 39–43b, 54), and thus they are difficult to see in the light microscope, especially on more heavily silicified valves. The marginal ring of strutted processes is evenly spaced, with no other processes on the valve except for the off-center labiate process. The labiate process is usually easily seen even on the most heavily silicified valves and is a distinctive feature. The lightly silicified form of this species has been illustrated by Hasle and Heimdal (1970: Figs. 39–43) and Johansen and Fryxell (1985: Figs. 56, 57). The more heavily silicified form was illustrated by Hustedt (1958: Figs. 44–46) from samples concentrated by *Salpa fusiformis*.

Very lightly silicified valves from field collections have as many as nine (Fig. 1) to 12 (Fig. 2) fascicles or bundles of areola with the central row reaching the central cluster of strutted processes, similar to *Thalassiosira tumida* (Janisch) Hasle (Fryxell 1988). More heavily silicified valves (Figs. 3, 4) have eight or fewer fascicles, and those thus far seen in the sediments are either completely linear (with lines of areolae intersecting each other at angles of 60° or occasionally sublinear because of minor irregularities (unpublished observations). The general process patterns and fine structure of processes are constant from one form to the other, and the areola patterns change within the limits of fasciculated to linear, correlated to the degree of silicification.

Although living clones of *T. ritscheri* have been isolated, they have proved difficult to maintain in the culture conditions thus far utilized in this laboratory (unpublished observations). In the field, it is lightly silicified during rapid growth in the austral spring (personal observations), and chains connected by the central stiff, intertwined, rope-like threads resemble the better known *T. tumida* (El-Sayed 1971; Hasle et al. 1971). In the water column, a gradation of silicification can be seen as has been previously reported for *T. tumida* from culture raised at slightly different temperatures (Fryxell 1988). Thus it now appears that *T. tumida* and *T. ritscheri* both have lightly silicified austral spring and summer forms and more heavily silicified winter forms. The lightly silicified forms of both species have a fasciculated areola pattern, and the heavily silicified forms have linear to sublinear patterns. However, the general process patterns and the fine structure of the processes are species specific. It is probable that the reports of the warm water species *Thalassiosira leptopus* (Grunow) Hasle et G. Fryxell (as *Coscinodiscus lineatus*) from Antarctic sediment include observations of *T. ritscheri*.

Thalassiosira gracilis (Karsten) Hustedt was described by Karsten (1905:78) as a species of *Coscinodiscus* with a wide margin. The specimen he illustrated (Pl. III, Fig. 4) is intermediate in silicification. Hustedt (1958:109–110, Figs. 4–7) transferred the heavily silicified stage from *Coscinodiscus* to *Thalassiosira*. His samples were taken from the shrimp-like *Euphausia* in Antarctic waters to the South Atlantic (69° S–41° S) and from the plankton from 66° S–46° S, although it was more common from 64° S–61° S. He described the lightly silicified form as *T. delicatula* (p. 110, Figs. 8–10), which he found to be very common in *Salpa fusiformis* in the Antarctic waters from 69° S. Since this name is a later homonym in the genus, the species was renamed *T. expecta* Van Landingham (1978, p. 3394). Fryxell and Hasle (1979), noting the same fine structure of the

processes in the two taxa but not seeing intermediate forms in their materials, reduced *T. expecta* to varietal status.

Gradations have been seen repeatedly from the surface 200 m from field collections (Figs. 5–13). Heavily silicified valves have a wide margin, and the larger areolae on the center of the valve are more easily noted in the light microscope than the marginal ring of strutted processes (Figs. 5, 6). The nearly central strutted process is smaller than the central areolae, and the inconspicuous labiate process is at the edge of the smaller areola near the margin on the opposite side of the central area. With a lower degree of silicification, the central area still retains some coarseness and increased silicification (Figs. 7, 8). The marginal septum can be focused through so that the operculate nature of the strutted processes is more apparent (Fig. 9, broken valve). With even less silicification, the areolae are more evenly spaced across the valve and the marginal processes are more evident (Figs. 10, 11). On lightly silicified valves, the central areola and process remain relatively well silicified (Figs. 12, 13).

The heavily silicified form is found in the sediments (personal observations). It should also be noted that there are more records of the nominate variety in the plankton, possibly because it is distinctive and easily seen in light microscopy in spite of its small size, or because it is heavily silicified and is eroded more slowly. This species has germinated in culture from fecal pellets (unpublished observations), but since it was not the dominant species and too small for effective isolation by traditional methods, it has not been maintained in culture.

From field observations it appears at this time that the varieties as described in Fryxell and Hasle (1979) are growth stages of one species and will not prove to be valid taxonomically, although certainly of interest ecologically. Hustedt (1958) noted slight differences in spacing of the marginal processes between these stages, although Fryxell and Hasle (1979) could not confirm that these differences were consistent. The fine structure of the processes may be a more reliable character. The decrease in size with decrease in silicification, as shown in Figures 5–13, may be a reflection of cyclic sexual reproduction, an artifact of preservation, or random chance. Fryxell and Hasle (1979) list a range of 5–28 μm diameter for what they considered the heavily silicified nominate variety and 7–17 μm for the lightly silicified variety they called *T. gracilis* var. *expecta*.

Discussion

In the waning light and increasing storms of the Antarctic autumn and the hostile environment of the winter, survival over that extended period of stress, including some periods of high grazing pressure, can depend upon adaptations that would provide little advantage during high light and increasing stratification of summer conditions. With winter turbulence, the ever-present danger of sinking out of the surface waters takes on less importance, but a stored energy source and lower metabolism for survival during periods of darkness and a heavy theca resistant to breakage over the weeks between cell divisions (or even going through the gut of a grazer) is of paramount importance. Each of the three kinds of heavily silicified valves discussed below have these evolutionary advantages for survival in the hostile conditions of the polar autumn and winter; the specialized winter growth stages and the heavily silicified winter stages can be seen as alternatives to resting spores and also have the capability of multiple cell divisions when swept into lighted waters for short periods. Thus not only can some of the cells survive during the darkest months, but there is a possible increase in the breeding stock before the austral spring.

The best known of these heavily silicified cells, resting spores, can be found occasionally in appreciable numbers at the end of a bloom (Fryxell et al. 1979), but resting spores are not common in Antarctic waters (Hargraves and French 1983, Table 1). Those that are known include some species in the genera *Chaetoceros*, *Porosira*, *Thalassiosira*, *Odontella*, and *Stellarima* (e.g., Stockwell 1991; Villareal 1981; Syvertsen 1979, 1985; Hoban et al. 1980; Villareal and Fryxell 1990). The pattern that one can expect from resting spore formation includes: the vegetative theca is thrown off with or without rudimentary valves (See Fig. 34 in Fryxell et al. 1981); more heavily silicified resting spore cells are produced after a determinate number of divisions as singlets with rounded valves, heterovalvate doublets, or even occasionally as quadruplets with flattened intercalary valves; setae or external processes are reduced, thickened, or even missing, while the basic nature of strutted or labiate processes remain the same internally; cingular bands are missing in Chaetoceraceae or reduced in other taxa, and spores germinate into lightly silicified vegetative forms.

A winter growth stage is exemplified by *Eucampia*, both the northern variety, *E. antarctica* var. *antarctica*, and the southern variety, *E. antarctica* var. *recta* (Fryxell and Prasad 1990). When the winter stage is triggered, apparently at least in part by temperature changes, heterovalvate doublet winter stage cells are formed, and the vegetative cell is thrown off as for a resting spore (Fryxell and Prasad 1990). But instead of the cell being packed full of lipids, it remains vacuolate. Far under the ice, only the doublet cells can usually be found (personal observations). When light conditions at the ice edge and away from the ice in the open ocean allow some growth, the heterovalvate doublet cells reproduce into long chains of heavily silicified winter stage cells without germination into the summer form. From the sediments, winter growth has been estimated at 0.5 doublings in Prydz Bay, Antarctica, with only a few weeks without ice cover, to 6.5 doublings over the northern Kerguelen Plateau (Fryxell 1991).

Odontella litigiosa represents the summer stage of another diatom (Hoban et al. 1980). Since the heavily silicified form of *Odontella litigiosa* (as *Biddulphia anthropomorpha*) has been seen inside *B. litigiosa*, like a resting spore, according to Frenguelli and Orlando (1958) and Mangin (1915), there may be a parallel to *Eucampia* in winter growth stage. The different forms could explain the different observations in the literature.

Other distinctive winter growth stages are seen in *Rhizosolenia curvata* Zacharias and *R. alata* Brightwell (or *Proboscia alata* (Brightwell) Sundström) (as illustrated in El-Sayed and Fryxell 1991, Pl. VIII, Figs. 1, 4). They noted a distinctive morphology in winter, with preliminary evidence that the cells continue to divide. Thus far, the heavily silicified winter stage cells of *R. curvata* have been noted only on end valves, whereas in *R. alata* winter cells were found reproducing themselves.

The variability of *Thalassiosira tumida* was noted by Hasle et al. (1971), with a listing of the taxa having similar morphology that suggest synonymy. Variable species are likely to have been described more than once, especially in remote Antarctic water with brief, disjunct observations, but discontinuous variability has proved valuable in ascertaining different genetic stocks in the field. By utilizing living cultures, conserved morphological features have been demonstrated. In this case, the fine structure of the processes and the general process patterns (as suggested first and outlined by Hasle 1968) have been conservative; the areolar pattern varied from sublinear to fasciculated (Fryxell 1988), and scanning electron and light micrographs have shown the corresponding different degrees of silicification (Hasle et al. 1971). Since fasciculation can be quantified, it is of value in analyzing responses to environmental changes. In this case, the degree of fasciculation has been positively related to temperature.

As reported above, the same kind of response has been noted in the field for *T. ritscheri* as for *T. tumida*, and the growth in spring and summer produces lightly silicified forms. There could be factors other than temperature also involved, but the heavily silicified forms are produced in the autumn and winter.

Another fasciculated species, *T. maculata* Fryxell et Johansen (Johansen and Fryxell 1985:170–173, Figs. 72–74, 77–80) was described from 46° S in the Indian Ocean. The fine structure of the processes is distinctive, with longer portions of the strutted processes extending internally and with marked opercula over the satellite pores. There are several strutted processes scattered on the face of the valve and a ring of processes around the margin. The single labiate process on each valve has the slit parallel to the margin and is in the marginal ring of strutted processes. Hustedt (1958:112, Figs. 26–28) considered this species to be *Coscinodiscus bullatus* Janisch. However the type material of that species has been examined, and that material is not a species of *Thalassiosira*.

The fine structure of the processes and the general process pattern is the same as *T. oliverana* (O'Meara) Makarova et Nikolaev (1984:89, 90, 2 pls.), which has many characteristics of a resting spore, with its heavily silicified structure and externally raised area surrounding the labiate process (Makarova 1988: Pl. XVII, Fig. 10). Makarova and Nikolaev (1984) reviewed its complex nomenclature and recognized that it belongs in the genus *Thalassiosira*. From a recent study of past collections (Hasle and Fryxell, unpublished) and in the light of repeated field observations of living material, it now appears that *T. oliverana* is the winter stage of the diatom described as *T. maculata*, and the name with priority is *T. oliverana*.

Thalassiosira gracilis also has many of the appearances of a resting spore, but no evidence of spore formation has been found. In addition, the intermediate forms suggest that it, too, is a winter stage with a more lightly silicified and less well-known summer stage. The name with priority is *T. gracilis*, and the degree of silicification is of ecological interest.

Even the pennate diatoms may have some differences in degree of silicification. *Nitzschia kerguelensis* was recognized as having coarse and finer structure by Van der Spoel et al. (1973: Pl. 1, Figs. a, b). El-Sayed and Fryxell (1991: Pl. IV, Fig. 4) illustrate a chain of this species with heavier terminal valves, as if a winter form were germinating, a feature previously noted in rough cultures (unpublished observations). Thus the winter stage does not seem to be a feature limited to centric diatoms.

In *Porosira* the capability of making resting spores has been proved in culture (Villareal 1981; Villareal and Fryxell 1990), but there also is a colder water form (Villareal and Fryxell 1983). *Stellarima microtrias* (Ehrenberg) Hasle et Sims has a distinctive spring and summer stage of inflated, drum-shaped cells put together in long chains with apparently random attachment points (Fryxell 1989). Resting spore production of *Stellarima* is well illustrated by Syvertsen (1985; also see Fryxell 1989), but there appears to be a heavily silicified form that continues winter growth as well (personal observations). Thus some species appear to have the capability of making both resting spores and heavily silicified winter stages (Table 1). The production of winter growth stages is a relatively common, although not universal, feature in Antarctic water. The physiological changes have yet to be explored and compared to those of resting spores as in Doucette and Fryxell (1983).

General Patterns Seen

These three kinds of heavily silicified valves in the sediment provide somewhat different kinds of information (Table 1). The abundance of resting spore valves in the sediment

can give a reasonable estimate of the population size averaged over seasonal cycles during the time of sedimentation. But the abundances of the two different kinds of winter growth stages give a more complicated paleoecological signal, since they are the result not only of the size of the population at the onset of winter but also of the amount of growth during the winter. At that time light is limiting, not only as a result of the oblique light, short days, cloudy skies, the depth of winter mixing, but also from the extent and duration of ice cover. Thus, high abundance of a winter stage of a taxon indicates productivity during a time of marginal growth at the ice edge or in the open water. In those areas the diatoms that form heavily silicified winter stages apparently have an evolutionary advantage over those that form resting spores. They also record an alternative life history and at least marginal growing conditions instead of a completely hostile environment.

TABLE 1. Examples of heavily silicified life stages in Antarctic waters.

Resting spores	
Lacking cingula	
Hyalochaetae section of *Chaetoceros*	
With modified cingula	
Odontella weissflogii	
Thalassiosira antarctica, *T. scotia*, *T. australis*, *T.* sp. cf. *gravida*	
Winter growth stages	
Modified vegetative morphology	
Eucampia antarctica	
Nitzschia kerguelensis	
Odontella litigiosa	
Rhizosolenia alata, *R. curvata*	
Gradational changes	
Phaeoceros section of *Chaetoceros*	
Thalassiosira tumida, *T. ritscheri*, *T. oliverana*, *T. gracilis*	
Both resting spores and winter growth stages	
Porosira pseudodenticulata, *P. glacialis*	
Stellarima microtrias	

Acknowledgements

I appreciate helpful discussions with T. K. Ashworth, J. G. Baldauf, M. A. Hoban, S-H. Kang, and A. K. S. K. Prasad. P. A. Fryxell edited a draft of the manuscript. Partial funding has been received from the Department of Oceanography, TAMU; N. S. F. Grant DPP-84-18850, and ODP Grant 20200, and this support is gratefully acknowledged.

Literature Cited

BARRON, J. A. AND B. LARSON, WITH SHIPBOARD PARTY. 1989. Proceedings of the Ocean Drilling Program, Initial Reports 119, Kerguelen Plateau-Prydz Bay, 14 December 1987–20 February 1988. Ocean Drilling Program, Texas A & M University, College Station, Texas.

DOUCETTE, G. J. AND G. A. FRYXELL. 1983. *Thalassiosira antarctica*: vegetative and resting stage chemical composition of an ice-related marine diatom. Mar. Biol. 78:1–6.

EL-SAYED, S. Z. 1971. Observations on a phytoplankton bloom in the Weddell Sea. Pp. 301–312 *in* Biology of the Antarctic Seas IV, G. A. Llano, ed. American Geophysical Union, Washington, D. C.

EL-SAYED, S. Z. AND G. A. FRYXELL. 1991. Phytoplankton. *In* Antarctic Microbiology, I. Friedmann, ed., John Wiley & Sons, New York. In press.

EPPLEY, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70:1063–1084.

———. 1977. The growth and culture of diatoms. Pp. 24–64 *in* The Biology of Diatoms, D. Werner, ed. University of California Press, Berkeley.

FRENGUELLI, J. AND H. A. ORLANDO. 1958. Diatomeas y sillico- flagelados del Sector Antárctico Sudamericano. Inst. Antártico Argentino Publ. 5:1–191.

FRYXELL, G. A. 1977. *Thalassiosira australis* Peragallo and *T. lentiginosa* (Janisch) G. Fryxell, comb. nov.: two antarctic diatoms (Bacillariophyceae). Phycologia 16:95–104.

———. 1988. Polymorphism in relation to environmental conditions as exemplified by clonal cultures of *Thalassiosira tumida* (Janisch) Hasle. Pp. 61–73 *in* Proceedings of the 9th Diatom Symposium 1986, F. E. Round, ed. BioPress Ltd and Koeltz Scientific Books, Bristol and Koenigstein.

———. 1989. Marine phytoplankton at the Weddell Sea ice edge: seasonal changes at the specific level. Polar Biol. 10:1–18.

———. 1991. Comparison of winter and summer growth stages of the diatom Eucampia antarctica from the Kerguelen plateau and south of the Antarctic convergence. Proceedings of the Ocean Drilling Program, Scientific Results, Leg 119, J. A. Barron and B. Larsen, eds., College Station, Texas. In press.

FRYXELL, G. A., G. J. DOUCETTE, AND G. F. HUBBARD. 1981. The genus *Thalassiosira*: the bipolar diatom *T. antarctica* Comber. Bot. Mar. 24:321–335.

FRYXELL, G. A. AND G. R. HASLE. 1979. The genus *Thalassiosira*: species with internal extensions of the strutted processes. Phycologia 18:378–393.

FRYXELL, G. A. AND A. K. S. K. PRASAD. 1990. *Eucampia antarctica* var. *recta* (Mangin) stat. nov. (Biddulphiaceae, Bacillariophyceae): life stages at the Weddell Sea ice edge. Phycologia 29:27–38.

FRYXELL, G. A., T. A. VILLAREAL, AND M. A. HOBAN. 1979. *Thalassiosira scotia*, sp. nov.: observations on a phytoplankton increase in early austral spring north of the Scotia Ridge. J. Plankton Res. 1:355–370.

HARGRAVES, P. A. AND F. W. FRENCH. 1983. Diatom resting spores: significance and strategies. Pp. 49–68 *in* Survival Strategies of the Algae, G. A. Fryxell, ed. Cambridge University Press, Cambridge.

HART, T. J. 1942. Phytoplankton periodicity in Antarctic surface waters. Discovery Repts. 21:261–356.

HASLE, G. R. 1968. The valve processes of the centric diatom genus *Thalassiosira*. Norw. J. Bot. 15:192–201.

HASLE, G. R. AND G. A. FRYXELL. 1970. Diatoms: cleaning and mounting for light and electron microscopy. Trans. Am. Microsc. Soc. 89:469–470.

HALSE, G. R. AND B. R. HEIMDAL. 1970. Some species of the centric diatom genus *Thalassiosira* studied in the light and electron microscopes. Nova Hedwigia, Beih. 31:543–581.

HASLE, G. R., B. R. HEIMDAL, AND G. A. FRYXELL. 1971. Morphological variability in fasciculated diatoms as exemplified by *Thalassiosira tumida* (Janisch) Hasle, comb. nov. Pp. 313–333 *in* Biology of the Antarctic Seas IV, G. Llano, ed. American Geophysical Union, Washington, D. C.

HOBAN, M. A., G. A. FRYXELL, AND K. R. BUCK. 1980. Biddulphioid diatoms: resting spores in Antarctic *Eucampia* and *Odontella*. J. Phycol. 16:591–602.

HUSBY, D. M., R. D. MUENCH, AND J. T. GUNN. 1989. Oceanographic observations in the Scotia Sea Marginal Ice Zone June–August 1988. NOAA Technical Memorandum NMFS SWFC 127:20–47.

HUSTEDT, F. 1958. Diatomeen aus der Antarktis und dem Südatlantik. Deutsche Antarktische Expedition 1938/1939. 2:110–192.

JOHANSEN, J. R. AND G. A. FRYXELL. 1985. The genus *Thalassiosira* (Bacillariophyceae): studies on species occurring south of the Antarctic Convergence Zone. Phycologia 24:155–179.

KANG, S. H. 1989. Diatom species composition and abundance in water column assemblages from five drill sites in Prydz Bay, Antarctica, Ocean Drilling Program Leg 119: distributional patterns. M.S. Thesis, Texas A & M University, College Station, Texas.

KANG, S. H. AND G. A. FRYXELL. 1991. Most abundant diatom species in water column assemblages from five ODP Leg 119 drill sites in Prydz Bay, Antarctica: distributional patterns. *In* Proceedings of the ODP Scientific Results, 119, Barron, J., Larsen, B. et al., College Station, Texas. In press.

KARAYEVA, N. I. AND S. K. DZHAFAROVA. 1988. Morphology of some polyhalobic diatoms in connection with changes in salinity. Bot. Zh. 73:477–485.

KARSTEN, G. 1905. Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898–1899. Deutsche Tiefsee-Expedition 1898/99 2:78–143.

LI, C.-W. AND Y-M. CHIANG. 1979. A euryhaline and polymorphic new diatom, *Proteucylindrus taiwanensis* gen. et sp. nov. Br. phycol. J. 14:377–384.

MAKAROVA, I.V. 1988. Diatoms of the marine algae of the U. S. S. R.: the genus *Thalassiosira* Cl. Akademia Nauk S. S. S. R. 117 pp.

MAKAROVA, I. V. AND V. A. NIKOLAEV. 1984. Notes on the genus *Schimperiella* (Bacillariophyta). Bot. Zh. 69:87–90.

MANGIN, L. 1915. Phytoplankton de l'Antarctique. Expedition du POURQUOI PAS? Deuxieme Expedition Antarctique Francaise (1908– 1910) commandee par le Dr. Jean Charcot. Paris. 95 pp.

NELSON, D. M., W. O. SMITH, L. I. GORDON, AND B. H. HUBER. 1987. Spring distributions of density, nutrients, and phytoplankton biomass in the Ice Edge Zone of the Weddell-Scotia Sea. J. Geophys. Res. 92:7181–7190.

NEORI, A. AND O. HOLM-HANSEN. 1982. Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. Polar Biol. 1:33–38.

PAASCHE, E. 1980. Silicon. Pp. 259–284 *in* The Physiological Ecology of Phytoplankton, I. Morris, ed. Studies in Ecology 7. Blackwell Scientific Publications, Oxford.

PAASCHE, E., S. JOHANSSEN, AND D. L. EVENSEN. 1975. An effect of osmotic pressure on the valve morphology of the diatom *Skeletonena subsalsum* (A. Cleve) Bethge. Phycologia 14:205–211.

SCHULTZ, M. E. 1971. Salinity-related polymorphism in the brackish-water diatom *Cyclotella cryptica*. Can. J. Bot. 49:1285–1289.

SIMONSEN, R. 1974. The diatom plankton of the Indian Ocean Expedition of the RV Meteor (1964–1965). Meteor Forschungs- Ergebnisse, Reihe D., 19:1–107.

STOCKWELL, D. A. 1991. Distribution of *Chaetoceros* resting spores in the Quaternary sediments from ODP Leg 119. *In* Barron, J., Larsen, B. et al. Proceedings of the ODP Scientific Results, 119, College Station, Texas.

SYVERTSEN, E. E. 1979. Resting spore formation in clonal cultures of *Thalassiosira antarctica* Comber, *T. nordenskioeldii* Cleve and *Detonula confervacea* (Cleve) Gran. Nova Hedwigia, Beih. 64:41–63.

———. 1985. Resting spore formation in the Antarctic diatoms *Coscinodiscus furcatus* Karsten and *Thalassiosira australis* Peragallo. Polar Biol. 4:113–119.

WILLIAMS, R. B. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. Ecology 45:877–880.

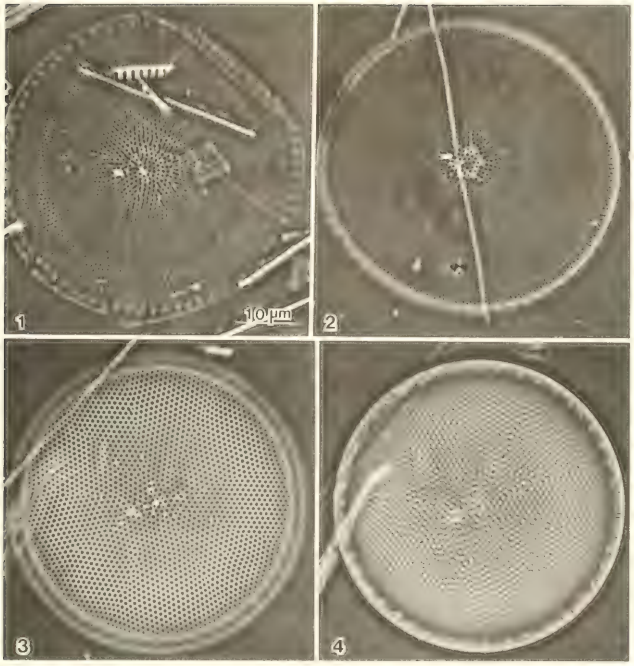
VAN LANDINGHAM, S. L. 1978. Catalogue of the Fossil and Recent Genera and Species of Diatoms and their Synonyms. Part VII: *Rhoicosphenia* through *Zygoceros*. Cramer, Hirschberg. Pp. 3606–4241.

VAN DER SPOEL, S., G. M. HALLEGRAEF, AND R. W. M. VAN SOEST. 1973. Notes on variation of diatoms and silicoflagellates in the South Atlantic Ocean. Netherlands J. Sea Res. 6:518–541.

VILLAREAL, T. A. 1981. The bipolar diatoms *Thalassiosira antarctica* Comber and *Porosira glacialis* (Grun.) Jørg. morphology and autecology of disjunct populations. M.S. Thesis, Texas A & M University, 110 pp.

VILLAREAL, T. A. AND G. A. FRYXELL. 1983. Temperature effects on the valve structure of the bipolar diatoms *Thalassiosira antarctica* and *Porosira glacialis*. Polar Biol. 2:163–169.

———. 1990. The diatom genus *Porosira* Jørg. Cingulum patterns and resting spore morphology. Bot. Mar. 33:415–422.



Explanation of Plates

Plate 1, Figures 1–4.
FIGURES 1–4. *Thalassiosira ritscheri* (Hustedt) Hasle taken on the Ocean Drilling Program Leg 119 service vessel in Prydz Bay, Antarctica, with vertical opening-and-closing net hauls. FIGURE 1. Site 740, Prydz Bay, Antarctica, 26 Jan. 1988, 200–100 m. Lightly silicified, flattened valve showing off-center labiate process and regularly spaced, near-marginal ring of strutted processes. Note nine fascicles reaching central strutted process grouping, each within an areola. FIGURE 2. Same location, 40–80 m. Focus on central cluster of strutted processes and near-center labiate process. Eleven fascicles reaching center cluster. FIGURES 3, 4. Same specimen with eight fascicles reaching central cluster, approaching a linear pattern. Site 739, 80–40 m, 29 Jan. 1988. FIGURE 3. Focus on areolae and near-center labiate process. FIGURE 4. Focus on internal strutted processes in near-marginal ring.

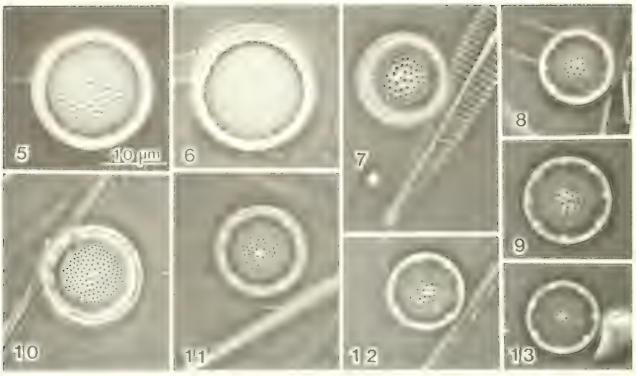


Plate 2, Figures 5–13

FIGURES 5–13. *Thalassiosira gracilis* (Karsten) Hustedt with gradations from the nominate variety to *T. gracilis* var. *expecta* Fryxell et Hasle, collected on the ODP Leg 119, Prydz Bay, Antarctica, vertical opening-and-closing net hauls with 35 µm mesh, except where noted. FIGURE 5. *T. gracilis* var. *gracilis*, Site 740, 40–0 m, 25 Jan. 1988. Focus on coarse areolae near center of heavily silicified valve. FIGURE 6. Same specimen, with focus on near-marginal ring of processes showing inside the wide marginal area. FIGURE 7. Site 741, 50–0 m, 29 Jan. 1988. Moderately silicified form with structure intermediate between the two varieties, focus on central areolae. FIGURE 8. Site 740, 0–200 m, 25 Jan. 1988. Intermediate form closer to that described for *T. gracilis* var. *expecta*. FIGURE 9. Site 741, 50–0 m, 29 Jan. 1988. Form with widely spaced processes and slightly increased silicification near center of broken valve. FIGURE 10. Site 740, 40–0 m, 25 Jan. 1988. *T. gracilis* var. *expecta*, focus on central areolae, slightly heavier than those near margin. FIGURE 11. Site 740, 50–0 m, 26 Jan. 1988. Valve with lightly silicified, continuous areolar pattern. FIGURE 12. Site 741, 200–0 m, 28 Jan. 1988, collected with an open 64 µm meshed net. FIGURE 13. Site 741, 50–0 m, 29 Jan. 1988. Delicately structured, lightly silicified valve.

Spatial and Temporal Diatom Relationships In the Lower James River, Virginia, U. S. A.

by

Harold G. Marshall

Department of Biological Sciences, Old Dominion University,
Norfolk, Virginia 23529

with 3 figures, 2 tables, and 1 plate

Abstract: Diatom composition and abundance were studied over a four-year period at stations within the tidal range of the James River. Distinct assemblages were associated with tidal fresh waters and the oligo-mesohaline sections of the river. The first group was dominated by *Skeletonema potamos*, *Aulacoseira* spp., and *Cyclotella striata*, which were replaced downstream as dominants by several estuarine species (e.g., *S. costatum*, *Leptocylindrus minimus*, *C. caspia*, and *C.* spp.). There was a trend for diatom maxima to reoccur during spring, summer, and fall. However, these maxima varied year to year as to their onset, magnitude, and duration. Nutrient concentrations decreased downstream, with a pattern of increased diatom concentrations noted at the tidal fresh water region.

Introduction

The James River is a major tributary of the lower Chesapeake Bay, which is located in the eastern coastal region of the United States. The river passes mainly through agricultural lands before its entry into the industrialized port-complex of Hampton Roads and the lower Chesapeake Bay. This study emphasizes the diatom assemblages within the tidal range of the lower James River, which is approximately 166 km in length. This is one of three river systems where phytoplankton populations have been monitored by Marshall and Alden (1990a), who described spatial and temporal assemblages and their relationships with salinity and nutrient concentrations. The spatial groups in the James River included tidal fresh water (less than 0.5 ‰), oligo-mesohaline, and mesohaline assemblages of mixed phytoplankton composition. At the Chesapeake Bay entrance to the James River, polyhaline conditions occur. Marshall and Alden (1990a) also noted a similarity in the seasonal successional patterns where differences were associated with spatial (site) effects. Major temporal influences accompanying the spring diatom development included the onset and duration of the seasonal rains. Filardo and Dunstan (1985) noted an inverse relationship between phytoplankton abundance in the upper oligohaline reach of the James River and biomass in the mesohaline section. They related nutrient dynamics in the oligohaline region of the James River to the development of the spring bloom downstream. Anderson (1986) found the oligohaline mixing region with increased nutrient levels and phytoplankton growth in several rivers, including the James. Further relationships between

specific nutrient concentrations and the development of different assemblages in the Chesapeake Bay were given by McCarthy et al. (1977) and by Hecky and Kilham (1988) for freshwater and marine habitats. Phytoplankton assemblages in the lower Chesapeake Bay were discussed by Marshall and Lacouture (1986) and Marshall and Alden (1990a). The objectives of this report are to identify the seasonal abundance patterns for diatom assemblages in the tidal range of the James River, and to make inter-annual comparisons of these maxima over a four year period.

Materials and Methods

This study was part of a long-term monitoring program of the lower Chesapeake Bay, and was based on collections made between March 1986 and May 1990 (Marshall and Alden 1990a, b). Two stations were established in the James River (TF 5.5, RET 5.2) and a third station (LE 5.5) established outside the entrance of the James River (Fig. 1). Monthly collections were taken at each station by a water pump and hose. A 15-liter composite sample was obtained over a series of depths from both above and below the pycnocline. From each of these composites a 500 ml subsample was fixed in Lugol solution for analysis. When a pycnocline was absent, the composite samples were taken from the upper and lower thirds of the water column. After 48 hours these subsamples were processed through a series of settling and siphoning procedures to obtain a 20–25 ml concentrate that was placed in a settling chamber and analyzed with an inverted plankton microscope. Cell counts were made at 315X and 500X, with a minimum count and random field approach to produce an 85 % accuracy estimate for cell concentrations (Venrick 1978).

Results and Discussion

The waters within the lower James River ranged from tidal fresh at station TF 5.5 and oligo-mesohaline at station RET 5.2, to polyhaline at the river entrance (LE 5.5). A total of 106 diatom taxa were identified within the tidal fresh and oligo-mesohaline sections of the James River (Marshall 1991). The characteristic diatoms in the tidal fresh waters included *Skeletonema potamos*, *Aulacoseira granulata*, *A. distans*, and *Cyclotella striata*. Other prominent species were *Asterionella formosa* and a variety of benthic pennates. However, these diatoms were replaced throughout the year at the downstream site by another diatom assemblage common to Station LE 5.5 and the lower Chesapeake Bay (Marshall and Alden 1990b). These estuarine species included *Cyclotella caspia*, *Cyclotella* spp., *Skeletonema costatum*, and *Leptocylindrus minimus*. The estuarine diatoms predominated above and below the pycnocline in the oligo-mesohaline and mesohaline regions of the river. Mean cell concentrations in the James River for several of the more abundant species are given in Table 1.

Seasonal patterns of diatom cell densities at stations in the James River from March 1986 to September 1989 are given in Figure 2. There was a general similarity to the occurrence of the spring diatom maxima at the stations, with greater abundance of cells at the oligo-mesohaline site. A distinct bimodal pattern of spring- fall maxima developed at station RET 5.2. In general, periods of abundance throughout the water column were similar. Cells above the pycnocline were often a mixture of freshwater and estuarine species, with composition in the bottom waters dominated by estuarine cells. At the tidal freshwater station there were lower concentrations, but more frequent diatom maxima, with a tendency for greater concentrations during spring, summer, and fall. Transport of estuarine species in the sub-pycnocline waters to the tidal freshwater station was not significant, nor was there a distinct pycnocline at this site. This condition resulted in mainly freshwater diatoms

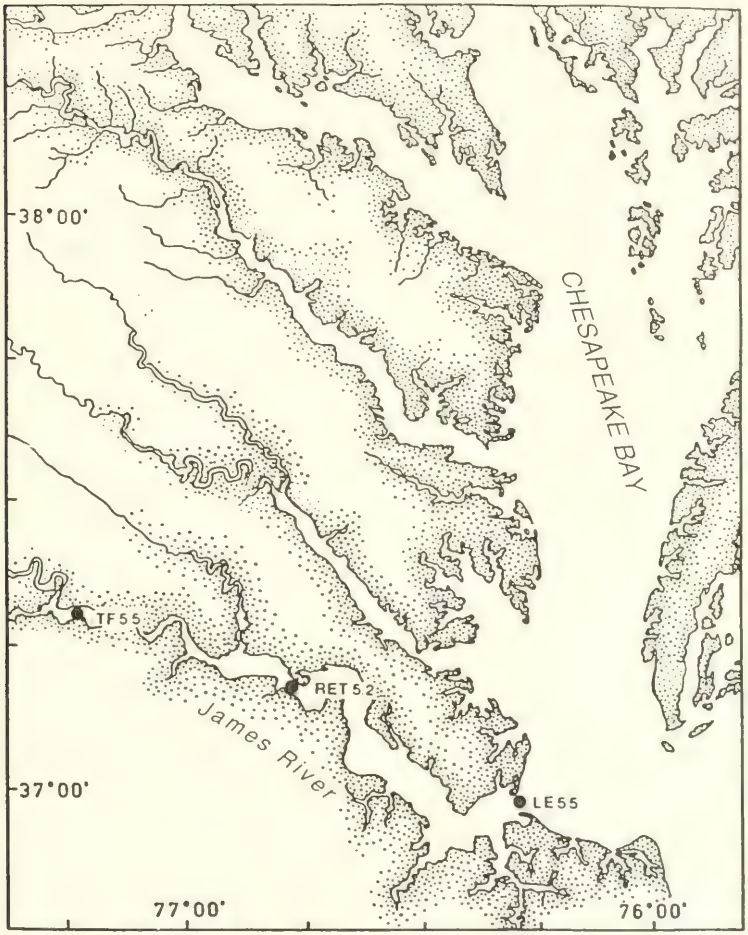


FIGURE 1. Station locations in reference to the lower Chesapeake Bay and James River.

throughout the tidal freshwater column. The general pattern downstream was for mean diatom abundance to increase from tidal fresh water ($5–6 \times 10^5$ cells/l) into the oligo-mesohaline region ($12–14 \times 10^5$ cells/l). Comparisons to mean diatom concentrations at station LE 5.5 for this same period indicate a lower abundance ($2–5 \times 10^5$ cells/l), which continued into the Chesapeake Bay (Marshall 1991). The peak development at the oligo-mesohaline site was a product of freshwater diatoms above the pycnocline, with a mixture

TABLE 1. Representative diatoms within the lower James River with mean concentrations (cells/l) between July 1986 and May 1990.

I. Tidal Fresh water	
Asterionella formosa Hassall	3,982
Cyclotella striata (Kütz.) Grunow	79,021
Aulacoseira distans (Ehr.) Simonsen	185,836
Aulacoseira granulata (Ehr.) Simonsen	135,628
Aulacoseira granulata v. *angustissima* (O. Müll.) Simonsen	22,471
Aulacoseira islandica (O. Müll.) Simonsen	2,311
Skeletonema potamos (Weber) Hasle	1,999,134
II. Oligo-Mesohaline	
Asterionella glacialis Castracane	8,830
Cerataulina pelagica (Cleve) Hendey	15,262
Cyclotella caspia Grunow	3,159,488
Leptocylindrus minimus Gran	450,670
Nitzschia pungens Grunow	2,936
Rhizosolenia fragilissima Bergon	9,823
Skeletonema costatum (Grev.) Cleve	694,468

of freshwater and estuarine species below the pycnocline. However, there was a rapid decrease in the abundance of *S. potamos* (Fig. 4) in oligo-mesohaline and mesohaline waters downstream, and this was associated with the increased dominance of *Skeletonema costatum*, and other estuarine diatoms during the spring and fall maxima. In contrast, the major transitional diatoms downstream in summer were *Cyclotella* spp.

During this study there was also an increase in the total diatom concentrations at the tidal freshwater station (TF 5.5). This was in contrast to station RET 5.2, where mean diatom abundance was more constant. At both sites, seasonal maxima reoccurred throughout the year with the tendency for peaks in late winter to mid-spring (January–April), mid-summer (June–July), and late summer to fall (August–November). Early winter (December) was generally characterized as a period of minimal annual development. The onset, magnitude and duration of these peaks varied for each station. By combining these station data sets for diatoms in the James River, between January 1989 and May 1990, a tri-modal pattern of increased seasonal abundance occurred (Fig. 3). These maxima were in spring, summer, and fall.

Nutrient concentrations for the three stations generally decreased downstream. Representative values are given for the river stations in Table 2. These data indicated the highest concentrations of Total N (TN), NO_2, NO_3, Total P (TP), PO_4 and silica were consistently found in the tidal fresh river station TF 5.5, decreasing in the oligo-mesohaline region, with lowest values at the river entrance. Mean silica concentrations decreased rapidly downstream from 5.63 to 0.30 mg/l at stations TF 5.5 and LE 5.5 respectively. Silica levels less than 0.5 to 0.8 mg/l have been noted by Reid and Wood (1982) as limiting to diatom growth. Marshall and Alden (1990b) applied several statistical approaches in analyzing the total phytoplankton relationships to various water quality variables in the study of three rivers (including the James) that enter the Chesapeake Bay. They found that after the spring growth, nutrient concentrations declined into summer, with the late summer-fall growth associated with nitrogen limiting conditions at the upper reaches of

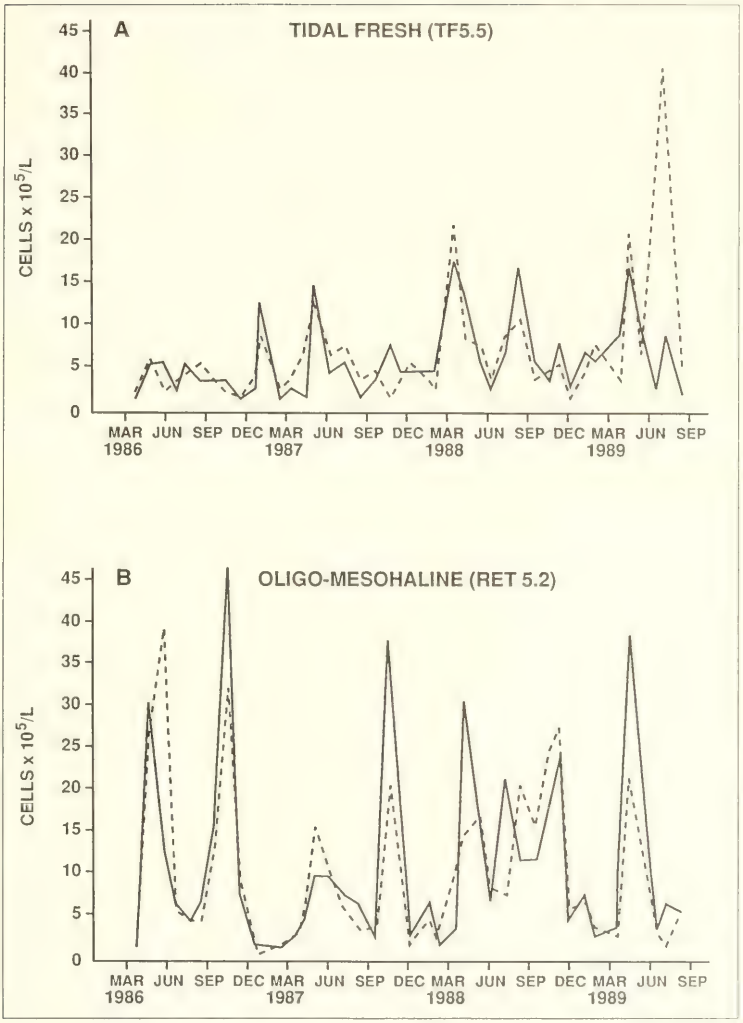


FIGURE 2. Mean concentrations of diatoms above (solid line) and below (dotted line) the pycnocline at A. The tidal fresh (TF 5.5) and B. The oligo-mesohaline (RET 5.2) stations in the James River from March 1986 through September 1989.

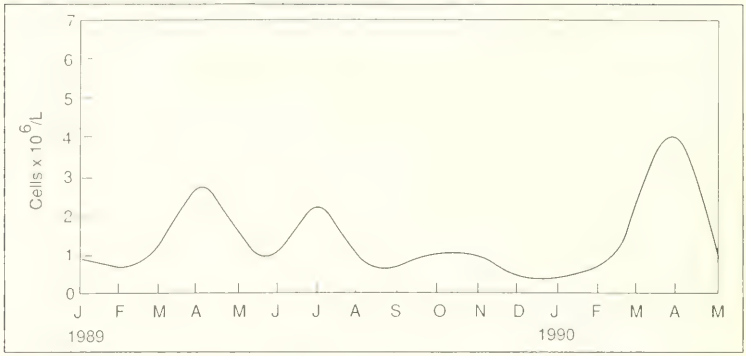


FIGURE 3. Combined mean concentrations above and below the pycnocline for diatoms between January 1989 and May 1990 for stations TF 5.5, RET 5.2, and LE 5.5.

TABLE 2. Mean water quality values (mg/l) for stations in the James River from November 1986 through June 1987.

Stations	TN	NO_2	NO_3	NH_4	TP	PO_4	Si
TF 5.5	0.89	0.059	0.507	0.026	0.16	0.045	5.63
RET 5.2	0.69	0.015	0.403	0.014	0.10	0.020	4.07
LE 5.5	0.55	0.009	0.042	0.045	0.06	0.015	0.30

the tidal rivers. However, downstream both nitrogen and phosphorus limiting conditions occurred. In addition, long-term trends in this data set were analyzed by Marshall and Alden (1991) in a series of non-parametric trend tests. These indicated there were significant trends of increased species diversity, an increase in cell concentrations both above and below the pycnocline, and an increase in nutrient concentrations in the James River. This trend for increased growth supports the abundance pattern depicted for station TF 5.5 (Fig. 2).

Conclusions

Results of this long-term monitoring study of diatoms at stations in the lower James River have identified two distinct assemblages. One was found in tidal fresh waters, the other was an estuarine assemblage, similar to the dominant species in the Chesapeake Bay, and distributed in the oligo-mesohaline regions of the river. A characteristic transition occurred moving downstream, with the dominant diatoms (e.g., *Skeletonema potamos*, *Cyclotella striata*, and *Aulacoseira* spp.) replaced by estuarine species (*S. costatum*, *C.* spp., etc.). Concentrations were rather evenly distributed in the water column, with sub-pycnocline waters downstream dominated by estuarine species and water above the pycnocline containing reduced numbers of tidal freshwater species that were mixed with estuarine dominants. Sub-pycnocline waters provided the transport for estuarine species into the tidal fresh and oligo-mesohaline sections of the river. The annual diatom assemblages at

one station, or the combined abundance data from several stations in the tidal river, typically had two to three annual growth peaks each year. These occurred in spring and fall, or spring, summer, and fall, with early winter (December) associated with reduced diatom numbers. These periods of growth varied annually as to their seasonal onset, magnitude, and duration. Highest nutrient concentrations were found upstream and the least at the river entrance. Diatom abundance initially increased from the tidal fresh to the oligomesohaline region, then cell abundance decreased downstream. This may be due in part to reduced nutrient levels available downstream (e.g., silica). The diatom maxima were the product of 8–10 % of the diatom species present within the river, with the other diatoms representing background species that were generally in low concentrations. Several characteristic and dominant genera within the tidal freshwater region were replaced by estuarine species of the same genus downstream.

Acknowledgements

This study was part of the lower Chesapeake Bay Monitoring Program sponsored by the Virginia State Water Control Board and the U. S. Environmental Protection Agency. Appreciation is given to Christine Phillips, Nancy Bland, Sean Morrison, and Lewis Affronti for their assistance and to personnel from ODU Applied Marine Research Laboratory and the State Water Control Board for providing water quality data used in the study.

Literature Cited

ANDERSON, G. 1986. Silica, diatoms and a freshwater productivity maximum in Atlantic coastal plain estuaries, Chesapeake Bay. Estuar. Coast. Shelf Sci. 22:183–197.

FILARDO, M. AND W. DUNSTAN. 1985. Hydrodynamic control of phytoplankton in low salinity waters of the James River estuary U. S. A. Estuar. Coast. Shelf Sci. 21:653–668.

HECKY, R. E. AND P. KILHAM. 1988. Nutrient limitation of phytoplankton in fresh water and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33:796–822.

MARSHALL, H. G. 1991. Preliminary results of phytoplankton composition, abundance and distribution in the lower Chesapeake Bay monitoring program. Sp. Rep. Old Dominion University Research Foundation, Norfolk, Va. 117 p.

MARSHALL, H. G. AND R. W. ALDEN. 1990a. A comparison of phytoplankton assemblages and environmental relationships in three estuarine rivers of the lower Chesapeake Bay. Estuaries 13:287– 300.

———. 1990b. Spatial and temporal diatom assemblages and other phytoplankton within the lower Chesapeake Bay, U. S. A. Pp. 311–321 *in* Proceedings of the 10th International Diatom Symposium, H. Simola, ed. Koeltz Scientific Books, Koenigstein.

MARSHALL, H. G. AND R. LACOUTURE. 1986. Seasonal patterns of growth and composition of phytoplankton in the lower Chesapeake Bay and vicinity. Estuar. Coast. Shelf Sci. 23:115–130.

MCCARTHY, J., W. TAYLOR, AND J. TAFT. 1977. Nitrogenous nutrition of the plankton in the Chesapeake Bay. I. Nutrient availability and phytoplankton preferences. Limnol. Oceanogr. 22:996–1011.

RIED, G. AND R. WOOD. 1976. Ecology of Inland Waters and Estuaries. Von Nostrand Co. New York, N. Y. 485 pp.

VENRICK, E. L. 1978. How many cells to count. Pp. 167–180 *in* Phytoplankton Manual, A. Sournia, ed. UNESCO.

Explanation of Plate

Plate 1
Specimens of *Skeletonema potamos* (Weber) Hasle collected from the James River in April 1988. Scale bars = 1 μm.

Diatom Stratigraphy and Environmental History of a Small Lake Basin in Southwest Norway. 1. The Last 4000 Years.

by

Solveig Aasheim

Botanical Institute, University of Bergen,
Allegt. 41, N-5007 Bergen, Norway

with 3 figures

Abstract: Lomtjørn is a small tarn near the west Norwegian coast. The area was farmed using traditional methods until 1972, when farming was abandoned. An oil refinery 3 km away started production in 1975.

After its isolation from the sea about 4000 BP, the original diatom flora of the lake was acidophilous. After forest clearance about 1500 BP and subsequent heath burning, some diatom taxa were replaced by taxa demanding a higher pH and nutrient status. When farming was abandoned, most of the original flora returned. By 1989, *Pinnularia abaujensis* var. *linearis* had become dominant in the benthic flora. Its increase may be indirectly caused by the cessation of the heath burning, or by an effect of the oil refinery. No effects of the industrial revolution in the form of acidification due to acid precipitation can be detected.

The most important event that has affected the diatom flora of Lomtjørn was the burning of the surrounding heath, resulting in the improvement of the nutrient status of the water.

Introduction

The Lomtjørn basin was first investigated by Kaland in connection with vegetation history (Bakka and Kaland 1971).

In 1970 it was decided an oil refinery would be built only 3 km away from Lomtjørn. Until then this area had been farmed in a traditional way with methods that had been more or less unchanged for hundreds of years. As part of an interdisciplinary project, we planned to describe the diatom populations present before the refinery started its production, and to do the same after some years to see if any change could be recorded. Besides monitoring the contemporary conditions in the tarn, I decided to analyze the lacustrine sediments, which cover the last 4000 years.

Kaland (1984) analyzed the fossil phytoplankton in the same sediments. He found that the lake had always been dystrophic and acidic.

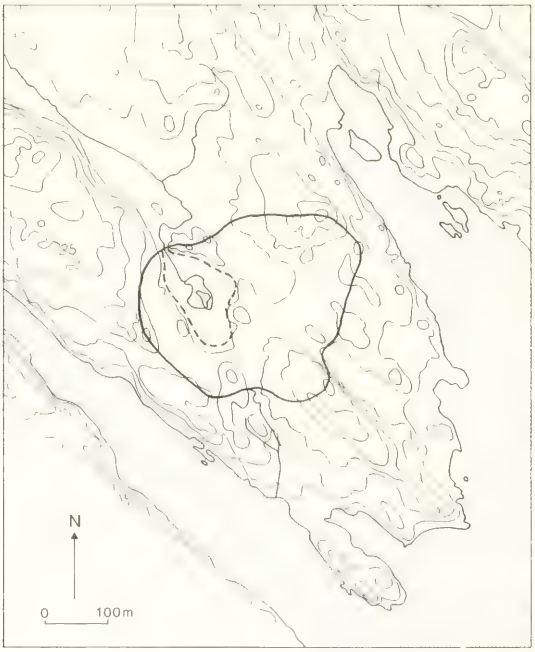


FIGURE 1. Map of the Lomtjørn area (60° 47'N, 4° 58'E) showing the catchment area (solid line), the area of the lake at the time of isolation from the sea 4000 years ago (dashed line), and the present size (whole line), when the surface is mostly covered with Sphagnum mats. The sea and the open water of the tarn are stippled.

Lomtjørn lies at 7.2 m above sea level, and the catchment area is ca. 8 ha. The bedrock is anorthositic gabbro that weathers slowly and produces a soil poor in nutrients.

When isolation from the sea took place 4000 years ago, the tarn was approximately 200 m long and 100 m wide. Today there is not much open water at Lomtjørn, as *Sphagnum* mats cover much of the surface. Water depth is around 3 m. The map (Fig. 1) shows the catchment area, open water at final isolation, and today's geographical setting.

Pollen analysis (Kaland 1986) shows that the forest was cleared by burning, and that farming began in the area at 1500 years BP. From then on heath was the dominant vegetation of the area. This heath was maintained by periodic burning. In addition, grazing throughout the year and cutting prevented forest growth. Woodland was only present as small patches, in localities out of reach of fire and grazing. For 1500 years the farmers continued to burn the heath, and in fact very little is known to have changed in the method of farming over the whole period. The heath in Lomtjørn's catchment area was burned for the last time in 1972. After that, parts of it were burned for scientific purposes in 1986.

Materials and Methods

A sediment core was obtained using a Livingstone corer of 110 mm diameter. Samples for analysis of fossil diatoms, pollen and phytoplankton were all taken from the same core. Diatoms were usually sampled at 20 cm intervals. Smaller intervals were used in some parts, where changes were presumed to have taken place. The ^{14}C date 4130 ± 120 BP is from Kaland (1984). Kaland (1986) showed that deforestation in this area occurred around 1500 BP. The date 1500 BP in Figure 2 is placed where pollen analysis of the same core shows deforestation.

Surface sediment samples were collected before the refinery started production (1971, 1972) and after (1987, 1988) using a Lundquist corer, excursion model (Lundquist 1936). The four uppermost samples in Figure 2 were collected with this device. Nomenclature follows Williams et al. (1988).

Results

Results of the analyses are presented in Figure 2. In this diagram the freshwater species are arranged in order of increasing pH preference, from left to right. Taxa that occur in few samples or in small quantities have been grouped according to the pH-optima published by the SWAP project (Birks et al. 1990).

The halophilous species disappeared at the base of the sequence (Fig. 2), and *Fragilaria virescens* var. *subsalina* flourished. Very soon this species gave way to a typical acidophilous freshwater flora.

Pinnularia abaujensis var. *linearis*, *P. brauniana*, and group E (optimum pH 5.30–5.67) appeared and increased rapidly when the basin was uplifted above sea level. *Eunotia rhomboidea*, *P. biceps* and group F (pH 5.75–6.16) were also present from the beginning of the freshwater phase. Some time later, *Aulacoseira distans* var. *nivalis* and *Frustulia rhomboides* var. *saxonica* also appeared, and both increased. These data confirm Kaland's (1984) view that the water was acidic and dystrophic from the beginning.

Twenty-five hundred years after the isolation of the lake, the percentage of *A. distans* var. *nivalis* suddenly dropped, together with percentages of *P. abaujensis*, *P. biceps*, and *F. rhomboides* var. *saxonica*. *Eunotia rhomboidea* also decreased slightly. *Fragilaria virescens* var. *exigua* expanded enormously and group F (pH 5.75–6.16) also increased. This assemblage continues to the top of the sediment core.

The analysis of recent material shows that in 1971 and 1972 *P. abaujensis* var. *linearis* increased, and since 1987 this taxon has dominated. *Pinnularia brauniana* was also favored by the conditions of the early seventies. Over the last few years diatoms grouped around pH 5.0–5.6 have increased or retained former relative abundance values, even though the pH measurement of the water was 4.5 in April 1989. Measurements during the years 1971–1989 showed a variation of pH from 4.2 (October 1971) to 4.9 (March 1973).

Discussion

The first large change in the diatom flora of the tarn occurred when the forest was cleared from the area at 1500 years BP (Fig. 2). *Pinnularia abaujensis* var. *linearis*, *Aulacoseira distans* var. *nivalis*, *Frustulia rhomboides* var. *saxonica*, and *Pinnularia biceps* showed a distinct and persistent negative reaction to the deforestation effects. *Fragilaria virescens* var. *exigua* and diatoms with pH preferences above 5.75 seemed to benefit from the change of conditions. When burning of the heath decreased from 1970 and was finally

FIGURE 2. Diatoms from the sediment in Lomtjørn. Freshwater taxa are arranged by increasing pH preference from left to right. The curves are calculated as percentages of the sum of ca. 300 diatoms. Some curves are exaggerated × 10. The depths (in cm) refer to depth below the water surface.

abandoned in 1972, all these diatoms reacted in the opposite way, except for *Aulacoseira*, which so far has not come back.

In a tarn such as Lomtjørn most of the nutrients in the water originate in the catchment. They are dissolved during leaching and are washed into the lake. Råen (1978) and Skogen (1989) have demonstrated an increase in available nutrients in the soil after the burning of heath in western Norway. After a few months, nutrient levels declined again. However, as the heath was traditionally burned during February and March, most of the nutrients were available during that growing season. In the deeper layers of the soil, levels of Ca, P and N remained higher for more than one year (Fig. 3A).

Skogen (1989) showed that pH in humus in western Norway was much higher after burning, and that this effect lasted for many years. Not until 10 years after burning didpH approach the levels of unburnt heath (Fig. 3B). In Finland, Rönkö et al. (1988) have shown how some diatoms in small streams react when the forest is clear-cut, *Eunotia rhomboidea* being the species that reacted most strongly. In the Finnish study, *E. rhomboidea* was severely reduced in abundance, but seemed to start to recover again after two years. In Lomtjørn this taxon also reacted to burning by dropping to a minimum for a period, but it recovered later.

Farming was abandoned in 1972, and in 1975 the refinery started production. None of the changes in the diatom flora before 1975 can be due to influence from the refinery. The increase of *Pinnularia abaujensis* var. *linearis* is, therefore, a response to the abandonment of burning in 1972. However, its increase in 1987 may be connected with the oil refinery. There has been little variation in pH during the years from 1971 to 1989.

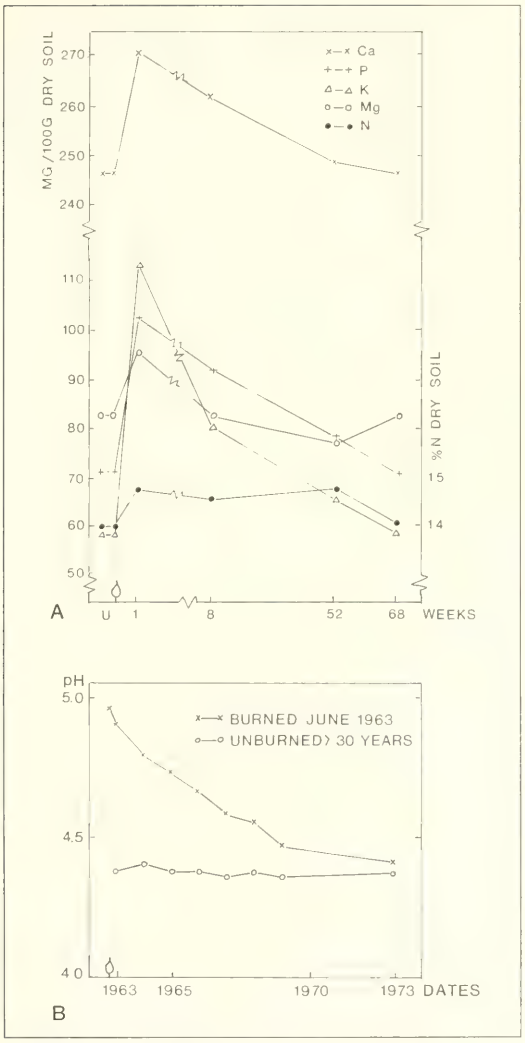


FIGURE 3. (A) Changes in the concentration of nutrients in the surface soil layer on burnt heath on Fusafjell (west Norway) through two vegetation periods. Redrawn after Råen in Skogen (1989). (B) pH in humus in burnt and unburnt heath on Hitra (west Norway) 1963–1973. Redrawn after Skogen (1989).

Thus the decrease of *P. brauniana* and the increase of group C and D taxa must have causes other than pH change.

In summary, it can be concluded that the change in the diatom assemblage 1500 years ago was caused by an increased influx of nutrients to the lake as a result of forest clearance and subsequent continued burning of the heath. The changes in the recent flora are due to the slow change in nutrient conditions after farming was abandoned. No significant changes in the diatom flora can be connected with the influence from last century's industrial revolution further south in Europe in the form of acid precipitation.

It is too early to predict how the diatom flora will react, if at all, to any local contamination from the oil refinery. In the autumn of 1989, a new, large refinery was started. The diatom flora in Lomtjørn will be closely monitored to study the effects of this new refinery.

Acknowledgments

I want to thank Knut Fægri and other colleagues in the Botanical Institute for information, comments, and practical assistance during the work with Lomtjørn. I want to especially thank Hilary Birks for scientific comments and linguistic revision of this paper.

Literature Cited

BAKKA, E. AND P. E. KALAND. 1971. Early farming in western Norway. Norw. Arch. Rev. 4.2:1–35.

BIRKS, H. J. B., J. M. LINE, S. JUGGINS, A. C. STEVENSON, AND C. J. F. TER BRAAK. 1990. Diatoms and pH reconstruction. Phil. Trans. R. Soc. London, B 327:263–278.

KALAND, P. E. 1984. Holocene shore displacement and shorelines in Hordaland, western Norway. Boreas 13:203–242.

———. 1986. The origin and management of Norwegian coastal heaths as reflected by pollen analysis. Pp. 19–36 *in* Anthropogenic indicators in pollen diagrams, K. E. Behre, ed. Balkema, Rotterdam/Boston. 246 pp.

LUNDQUIST, G. 1936. Sjösediment från mellersta Norrland. Inndalsälvens, Ångermannsälvens och Umeälvens vattenområden. Sveriges Geologiska Undersökning, C, 405. 152 pp.

RÅEN, S. C. 1978. Virkninger av lyngbrenning på vegetasjon og jordsmonn i subalpin lyngmark. Thesis. Univ. Bergen. 165 pp.

RÖNKÖ, J., H. SIMOLA, AND J. SIIRA. 1988. Effects of forest management on the benthic diatoms of small forest streams in East Finland. Pp. 109–114 *in* Proceedings of the Ninth International Symposium on Living and Fossil Diatoms, F. E. Round, ed. Biopress Ltd. and Koeltz Scientific Books, Bristol and Koenigstein

SKOGEN, A. 1989. Lyngheibrenning som viltstelltiltak for lirype og orrfugl. Fylkesmannen i Buskerud, Miljøvernavdelingen. Rapport No. 2:52–63.

WILLIAMS, D. M., B. HARDLY, R. ROSS, M. A. R. MUNRO, S. JUGGINS, AND R. W. BATTARBEE. 1988. A coded checklist of British diatoms. ENSIS Publishing, London. 74 pp.

Diatoms in Alkaline Peat: Preservation and Extraction

by

S. P. Main

Biology Department, Wartburg College, Waverly, Iowa 50677

with 2 tables and 1 plate

Abstract: During study of living and recent diatom associations in Minnesota peatlands, ashed peat samples were found to contain diatom remains. These peatlands are fens found in glacial moraine areas extending into the Lake Agassiz region.

Recent literature does not mention the usefulness of cleaning peat diatoms in the following fashion. The process developed consists of drying a peat sample at 80° C, ashing in a muffle furnace at 500° C, adding acid (hydrochloric or nitric) until gas release stops, and then preparing a rinsed diatom suspension. The resulting diatom suspension is cleaner than most acid treatments and generally more easily obtained.

The method of peat sample treatment for extracting diatoms was evaluated using split samples; one split was ashed in a muffle furnace and the other was treated with acid using standard procedures. Ashed peat samples when further treated with acid were found to yield diatom suspensions with less detritus than samples treated with acid only. Diatom taxa counts were comparable from such split samples.

The alkaline peat associations examined so far are dominated by *Denticula elegans* and *Epithemia argus*. Other abundant taxa include *Caloneis bacillum*, *Navicula minima*, *Nitzschia amphibia*, *Pinnularia appendiculata*, *Rhopalodia gibberula* v. *vanheurckii*. Other more delicately silicified diatoms are present, including species of *Achnanthes*, *Eunotia*, and *Fragilaria*..

Introduction

This research is part of a long-term ecological study of peatlands in northern Minnesota. Vascular plants, bryophytes, diatoms, and water chemistry are being sampled along a range of sites from the alkaline prairie fens of the Red River Valley (post-glacial Lake Agassiz) to the *Sphagnum*-dominated acid fens and bogs to the east. Permanent plots (relevés) are being established on protected natural areas. Peat cores are collected when dry or during the winter for analysis of recent floral distributions at these sites. Besides extending knowledge of plant distributions, this study will look for indications of climatic change in the very recent past.

During incineration of some plankton samples on a hot plate, Jan Janssens (the bryologist and chief peat corer on this project) asked whether ashed peat samples would retain

TABLE 1. Peat diatoms sampled from the Ogema prairie fen, Minnesota. Comparisons of incinerated (I), acid-cleaned (A), and incinerated followed by acid (I/A) extraction procedures

	Og22 22 cm I	Og25 25 cm I	6-26-89-7 25 cm A	6-26-89-8 38 cm A	OGM 8802-1 surface I/A	OGM 8802-1 surface A	OGM 8802-30 30 cm I/A	OGM 8802-30 30 cm A
Achnanthes lanceolata (Bréb.) Grun			1					
A. minutissima Kutz	1		5					
Caloneis bacillum (Grun.) Cl	6		11	6	27	20		1
C. ventricosa v. truncatula (Grun.) Meist			1					
Cyclotella comta (Ehrenb.) Kütz				2				
Cymbella microcephala Grun.					3	4		
C. perpusilla A. Cl					12	18		
C. sp. P1	2							
Denticula elegans Kutz.	98	10	32	6	284	225	22	8
Epithemia adnata v. porcellus (Kutz.) Patr	4	4	2	3				
E. argus (Ehrenb.)Kutz.	42	16	11	8	97	23	44	8
E. argus v. alpestris Grun			5		24	15	7	6
E. ocellata (Ehrenb.) Kütz					9	14		
E. turgida (Ehrenb.) Kutz		2					2	
E. sp. P1							2	
E. sp. P2							3	
Eunotia arcus Ehrenb. ?							3	1
E. curvata (Kutz.) Lagerst							4	
Fragilaria virescens Ralfs		2	2	3				
Gomphonema angustatum (Kutz.) Rabh			6	6				
G. dichotomum Kutz			1					
G. parvulum (Kutz.) Kütz								2
G. sp. P7							2	
G. sp. P8							2	
Mastogloia grevillei Wm. Smith							3	
M. smithii v. lacustris Grun			7					
Melosira sp. P1				1			1	

diatoms. Examination of ashed samples from preliminary work revealed diatom valves. These peat samples had been incinerated in a muffle furnace at 550° C, which is in the 500–600° C range recommended for incinerating diatom samples on a hot plate (Round et al. 1990). This raised the prospect of using ash remains of the peat analysis as the source of cleaned diatoms without having to prepare diatom samples using acid cleaning as recommended in the literature. Results of a series of tests of this possible technique are presented here.

TABLE 1, continued

	Og22 22 cm I	Og25 25 cm I	6-26-89-7 25 cm A	6-26-89-8 38 cm A	OGM 8802-1 surface I/A	OGM 8802-1 surface A	OGM 8802-30 30 cm I/A	OGM 8802-30 30 cm A
Navicula amphibola Cl							2	
N. bryophila J B. Peterson					1	15		
N. contenta Grun					4	3		
N. heufleri Grun	2		1					
N. minima Grun			22	2				
N. mutica v. undulata (Hilse) Grun				1				
N. notha Wallace			2		16	5		
N. potzgeri Reimer	2							
N. simplex Krasske ?							2	
N. subhamulata v. undulata Hust					2	4		
N. tenelloides Hust ?	7			4				
Neidium bisulcatum (Lagerst) Cl.								2
Nitzschia amphibia Grun.	6	3	31	18	23	64		6
N. denticula Grun			5	2				
N. hantzschiana Rabh			14					
N. paleacea Grun.	2		2	6				
N. radicula Hust					8	20		
N. vitrea v. P1			1					
Pinnularia appendiculata (Ag) Cl					23	24		
P. borealis Ehrenb		4						
P. undulata Greg ?	6		2					
Rhopalodia gibba (Ehrenb) O. Mull							7	
R. gibba v. ventricosa (Kutz.) V H								2
R. gibberula v. vanheurckii O. Mull.	8	2	5	2	43	26		
R. parallela (Grun) O. Mull. ?	3	2	9	5	42	30		
Synedra ulna (Nitz) Ehrenb.			2					
Total valves counted	189	45	180	75	618	510	106	36
Transects of cover slip counted	1	17	4	13	2	2	10	20

Materials and Methods

Samples came from peat cores collected during 1988 and 1989 from the Ogema Spring Prairie Fen, Becker County, Minnesota (GLO coordinates: W5 142N 42W 13SENE). Alkalinities (titration with 0.216 N HCl to pH 5.0) measured in water collected in pits at Ogema relevés in summer 1989 ranged from 5.8–10.0 meq/l. Core monoliths were collected by cutting ca. 15 cm square vertical sections with a bread knife, frozen, and then trimmed to 10 cm in the laboratory before slicing the vertical section into horizontal sections 1 cm thick. At present cores are being collected with a Hiller corer. All cores have been stored frozen.

Subsamples for ash-free dry weight determination and for plant analysis were removed from frozen sliced sections with a cork borer. These cylindrical subsamples can be processed directly or stored in 24-well plates sealed with parafilm for later use. The ash-free dry weight determination involves incinerating an oven-dried, weighed subsample in a muffle furnace at 550° C.

Diatoms were originally extracted by placing a dried and weighed subsample in concentrated nitric acid in a Kjeldahl flask and allowing the reaction to proceed at room temperature. Then the acid mixture was gently boiled for 35 minutes. This modification of the procedure in Foster and Fritz (1987) seemed necessary when initial diatom suspensions appeared debris-laden after 10 minutes of boiling. The diatom suspension was then rinsed by sequential settling for 12 hours, decanting, and resuspension until neutral. A portion of the diatom suspension was then mounted in Naphrax for microscopic examination using an Olympus BH microscope at 1000× oil immersion magnification.

Upon discovering diatom frustules in ashed samples (see samples Og 22 and Og 25 in Table 1), fresh peat samples from the same area were examined using the acid treatment procedure (see samples 6-26-89-7 and -8 in Table 1). As these were not part of the same core samples, it seemed appropriate to compare incineration and acid oxidation of peat subsamples from the same source. A monolith collected while frozen and maintained that way from the Ogema fen in February 1988 was subsampled to make this additional comparison.

Ashed peat samples appear to contain varying amounts of acid-reactive inorganic matter and often have fluffy clumps of diatoms and other debris. Treatment of ashed peat samples with hydrochloric or nitric acid at room temperature, followed by the usual rinsing of the diatom suspension should produce a cleaner diatom extraction. Since the ash needed to be suspended in water to spread the diatoms on the cover slip, it was hoped that this acid treatment might also improve the dispersion of diatoms on the cover slip.

Results

Diatom frustules were found at some depth in alkaline fens, however distribution was extremely irregular. Thirty-one diatom taxa were found in four peat core monoliths collected from the alkaline prairie fen at depths from 22–38 cm (Table 1). Samples Og 22 and Og 25 were suspensions of diatoms found in untreated ash. Of the 17 taxa in these ashed samples, four were not found in the acid-treated samples. Two other samples (Og 23 and 24) taken between the above two had too few diatoms to attempt counting. Comparable acid-treated samples came from peat monoliths collected 26 June 1989. The 26 diatom taxa found here included 13 not found in the ashed samples. Eight of these, however, were found in one of the acid-treated samples only. Differences between ashed and acid-treated samples, though large, were assumed to reflect variability among depths and locations within the Ogema fen rather than treatment effects.

To test the above assumption, peat subsamples obtained from monoliths from the surface and from 10-, 20-, and 30-cm deep were split into two parts. One part was incinerated at 550° C followed by room temperature acid treatment and the other part was boiled in nitric acid/sulfuric acid. The resulting surface counts (Table 1) yielded similar results in terms of taxonomic composition, relative proportions, and the character of the suspension on the coverslip. The 10- and 20-cm deep peat subsamples had too few diatoms to evaluate and so are not included in Table 1. Of the 20 taxa in the 30-cm subsamples, 11 were only in the ashed then acid-treated split, and five were only in the boiled acid split. The four taxa in common included three of the four most abundant taxa in the ashed/acid

split. The differences may be attributed in part to the small number of diatoms counted on the acid-treated slide, even though over twice as much surface area was examined. It should be noted that equal aliquots of sample were not always used; the intent was to produce a suspension with about equal density of all particles. This preliminary evaluation compared the ease of finding diatoms in the suspensions produced by both extraction techniques. Standard practices of using known quantities of suspension for the slides will be followed during the major study.

Photomicrographs illustrate a taxon found typically in the split surface sample given both acid only and ashed/acid treatments. The physical appearance does not appear affected by different treatments. These figures of *Denticula elegans* Kütz. also illustrate a series of form changes between var. *elegans* Kütz. and fo. *valida* Pedicino. All specimens came from the OGM 8802-1 surface sample. These forms range from 19–54 µm in length, have 3–5 costae per 10 µm and 18–23 striae per 10 µm (Table 2). Longer specimens exceed lengths reported for both taxa in Patrick and Reimer (1975). Striae density extends the upper limit described for var. *elegans* and exceeds that described for fo. *valida*.

TABLE 2. Comparison of descriptions of *Denticula elegans* Kütz. varieties in Patrick and Reimer (1975) with the form variation found in surface peat samples (OGM8802-1) from Ogema fen, Minnesota., U. S. A.

Feature	v. *elegans*	f. *valida*	Ogema forms
length range, µm	15–40	12–37	19–54
costae/10 µm	3–5	3–4	3–5
striae/10 µm	15–18	ca. 20	18–23

Discussion

Diatoms in peat survive incinerating at 550° C in as good a condition as when boiled in acid. After each treatment of the surface peat samples (OGM 8802-1 samples in Table 1) the same taxa were found. The shifts in relative abundance for each taxon may reflect variation within the subsamples. The dried peat cylinder split for each treatment was not homogenized or mixed in any way to avoid loss of material. However, destruction of frustules may be more likely in genera with lightly silicified or more porous frustules, although *Caloneis bacillum* and *Navicula notha* are counter examples. These considerations are part of the continuing analysis of this procedure.

The major difficulty when mounting dry ashed preparations was poor adhesion of frustules to the coverslip. This was overcome by suspension in water. Using cold acid treatment and rinsing produced a satisfactory suspension that was also cleaner.

This study suggests that diatom frustules survive better in alkaline cores than has been found to be true in acid peat cores in this region (Kingston 1982). Even in alkaline peats diatom frustules become less abundant with increased depth. Additional samples are being examined to ascertain whether diatom frustules persist in a broad enough range of peat conditions to make comparisons between historical assemblages and surface communities.

Early in this century, commercial extraction of diatomaceous earth from peat beds in Florida, U. S. A., involved incineration at temperatures of up to 800° C (Calvert 1930). Hanna (1933) reported that these diatoms were "somewhat warped." Moss has used incineration in a muffle furnace at 550° C on sediment samples from Strumpshaw Broad with satisfactory results (Moss 1979). It appears that this incineration technique is effective,

but that temperature needs to be closely controlled. Subsequent cold acid treatment to remove acid-soluble minerals works and is recommended instead of using higher temperatures to remove carbonates.

Acknowledgements

Support for this research came from an ancillary grant that is part of a Mellon Foundation grant to E. Gorham, University of Minnesota. Facilities at Lake Itasca Biological and Forestry Station, Lake Itasca, Minnesota, and at Wartburg College, Waverly, Iowa, were used. Special thanks go to J. Janssens, University of Minnesota, for the core samples and ashed samples used in this study, and to L. Owen, D. Parson, and L. Von Ruden, Wartburg College undergraduates, for technical assistance on the project. Thanks to James Solliday for bringing the history of the Florida peat industry to my attention. The suggestions of the reviewer were very helpful.

Literature Cited

CALVERT, R. 1930. Diatomaceous Earth. American Chemical Society Monograph No. 52. Chemical Catalog Co., New York. 251 p.

FOSTER, D. R. AND S. C. FRITZ. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. J. Ecol. 75:409–437.

HANNA, G. D. 1933. Diatoms of the Florida peat deposits. Ann. Repts. Florida St. Geol. Surv. 23/24:65–119.

KINGSTON, J. C. 1982. Association and distribution of common diatoms in surface samples from northern Minnesota peatlands. Nova Hedwigia, Beih. 73:333–346.

MOSS, B. 1979. Algal and other fossil evidence for major changes in Strumpshaw Broad, Norfolk, England in the last two centuries. Br. phycol. J. 14:263–283.

PATRICK, R. AND C. W. REIMER. 1975. The Diatoms of the United States. Vol. 2, Part 1. Acad. Nat. Sci. Phila., Monograph No. 13. 213 p.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms. Cambridge University Press, Cambridge. 747 p.

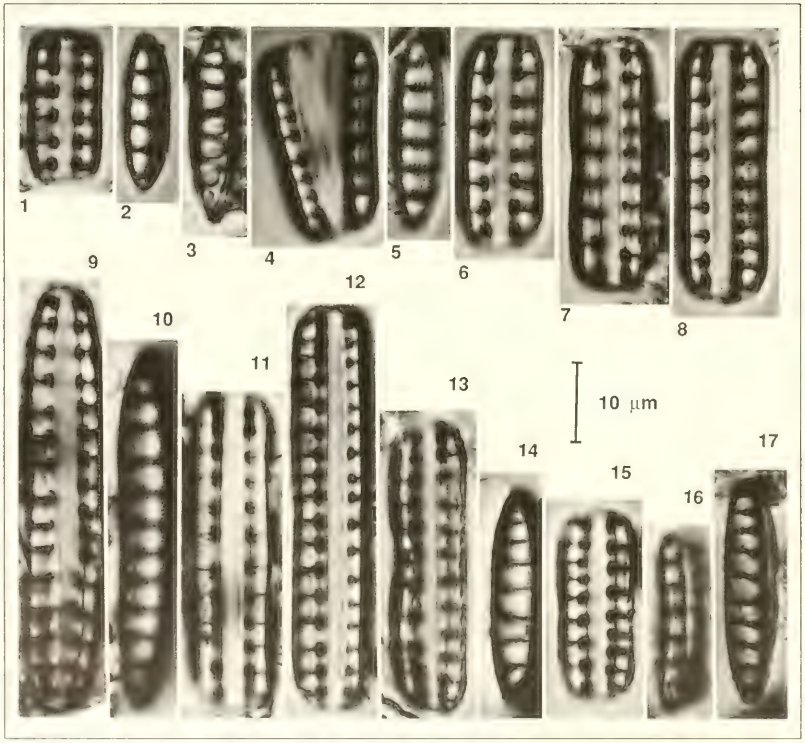


Plate 1, Figures 1–17
FIGURES 1–17. *Denticula elegans*, valve and girdle views from sample OGM8802-1 compared in Table 2. FIGURES 1–11. Acid extraction. FIGURES 12–16. Incineration/acid extraction. FIGURE 17. Septum from acid extraction.

Well-Preserved Diatoms in Limnic Opals of Hungary

by

E. Kovári-Gulyás

H-1025. Budapest, Szerena ut 51, Hungary

with 1 figure, 1 table, and 1 plate

Abstract: Miocene diatomaceous earth has been mined in the North-Hungarian Range for several decades. Limnic opal is interstratified in these diatomites and was used as a raw material for tools by prehistoric man. Examination of this raw material in thin section reveals common, well-preserved, even thin skeletons of diatoms.

In the Mátra Mountains at Szurdokpüspöki *Melosira bituminosa* var. *dilatata* dominates and occurs with *Navicula bituminosa* var. *robusta* and *Nitzshia frustulum* in limnic opals. In the Tokaj-Mountains at Erdobénye, a richer assemblage was identified in similar rock: *Melosira menilitica*, *M. arenaria*, *Stephanodiscus minutus*, *Amphora ovalis*, *Diploneis interrupta*, and *Epithemia subsalsa* were found, along with fragments of *Fragilaria*, *Rhopalodia*, and *Surirella* taxa.

These species are observed in the diatomaceous earth from both localities as well, indicating a limno-brackish paleoenvironment. In the case of Erdobénye, these diatom species were also found in adjacent freshwater lakes. The diatom flora present in stone-tool raw material can give useful, new information about the locality from which they were mined.

Introduction

In the Mátra and Tokaj Mountains, diatomaceous earth has been mined at Szurdokpüspöki and at Erdobénye. These diatomites were deposited in marine bays and in limnic basins during the Miocene. Within the layers of these deposits, limnic opal is found interstratified and is termed limno-opalite. It was used as a raw material for tools by prehistoric man. The limno-opalites studied in this investigation came from rock samples collected for the International Conference on Prehistoric Flint Mining and Lithic Raw Material Identification in the Carpathian Basin (held in Hungary in 1986). A comparison was made between the diatom assemblages of the limno-opalite and diatomites.

Materials and Methods

The limno-opalites that came from the archaeological assemblages near Budapest (Püspökszilágy, Veresegyháza) and in the North-Hungarian Range (Eger), were in use from the Middle Paleolithic to the Bronze Age, according to archaeologists (Biró 1988). They were mined in northern Hungary. The yellow-white-grey laminated limno-opalites were mined in Szurdokpüspöki and were found scattered in archaeological sites. The

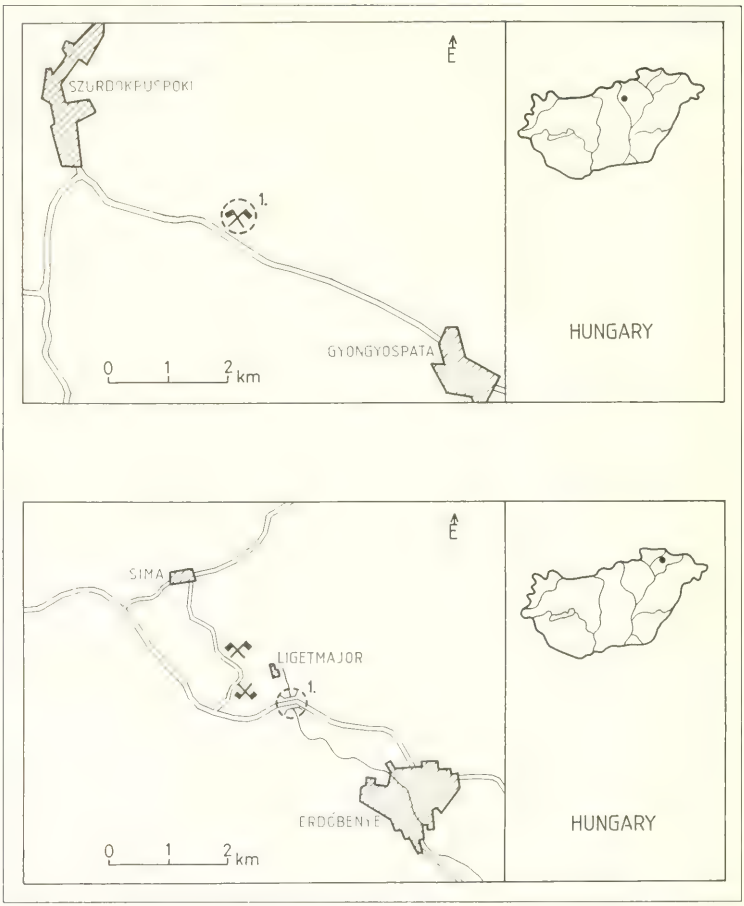


FIGURE 1. Localities of limno-opalites in Hungary.

Erdobénye-type of limno-opalite is mainly yellow, sometimes red. Archaeological pieces are known only from the environs of the source. These Neogene lithic raw materials are directly connected to the acidic-neutral volcanism that formed the inner arch of the Carpathians.

The volcanic rocks of Western Mátra consist of andesite and rhyolite tuffs. The most significant diatomaceous earth deposit in Hungary occurs at Szurdokpüspöki, and it overlies a pyroxenandesite tuff. This deposit was studied by Hajós (1968). It was formed in the Middle Miocene, at the boundary of the Carpathian/Badenian stages and at the beginning

of the Badenian. The diatomite could be divided into two parts: the lower ca. 45 m-thick beds were deposited in limno-brackish water, and the upper 50–60 m-thick beds settled in marine water. Between the two parts, there is a 25 m-thick rhyolite tuff intercalation. The lower layers of the diatomite are gray, clayey, bitumenic, and contain weathered tuffs. Yellowish-white and white diatomaceous earth increase gradually in the section.

At the boundary of the gray diatomite deposits and white diatomite, a 20–30 cm thick, continuous limno-opalite stratum is situated like a marker horizon. Its color is dark-gray, but it is yellow when oxidized. Previous examinations found it sterile with respect to siliceous microfossils.

In the gray, clayey diatomite several centimeters thick, interbeddings of limno-opalite can be found. Lenses of limno- opalite occur in the limno-brackish layers and show a continuous transition towards the white diatomite. Our latest examination of the opal material towards diatomite yielded identification of some diatom remains in it. The locality is shown on Figure 1.

Near Erdobénye at Ligetmajor, significant, thick tuffaceous clay, and mainly terrestrical rhyolite tuff with pumistone overlie the rough surface of pyroxenandesite. The upper horizon of this lithified tuff was overflowed several times with brackish water. Diatomaceous earth several meters thick was deposited in the depressions during the late Miocene, Sarmatian stage (Hajós 1959). The cover of it is limno-opalite, disintegrated into pieces of 1–5 m^3. There are only remains of aquatic plants in it. The limno-opalite we studied originated from the vicinity of the Ligetmajor mine at a bend in the road (Fig. 1). At this locality there is an outcrop with pieces of worked material scattered in the surface.

For the examination of siliceous microfossils about 10 g of rock were treated in hydrogen peroxide and in 1 L of concentrated sulphuric acid with a few drops of nitric acid, to eliminate organic contamination. For dissolving the clayey part, organic chemicals, e.g., Komplexon III or Selecton B, were used. For this procedure the rock must be broken into small pieces because of its high degree of hardness. Materials were examined partly in thin section and partly from strews.

Results

At the Szurdokpüspöki locality, diatoms are relatively well preserved in the limno-opalite. *Melosira bituminosa* var. *dilatata* is the most frequent taxon with other species occurring given in Table 1. The number of species is less in limno-opalite than in diatomite. They all suggest a shallow and limno-brackish water environment.

At the Erdobénye locality, diatoms were well preserved in the opal matrix. Preservation was so good that we could identify diatoms among pyrites and organic grains, even in thin sections (Plate 1). This occurrence is richer in species than the Szurdokpuspoki deposit. The most common species at Erdobénye are *Stephanodiscus minutus* and *Melosira menilitica* (Table 1). An abundance of double cells of *Epithemia* was observed. The diatom assemblage indicates that the paleoenvironment was limno-brackish, with freshwater lakes adjacent.

Discussion

Diatom occurrences in similar rocks are also known from other European countries, for example, in porcelanites of Polish Carpathians (Kotlarczyk 1966). In America, silica diagenesis and dissolution of diatom cells were studied in several cases (Hein et al. 1978).

TABLE 1. Relative abundance of diatoms in limno-opalites of Hungary.

	Szurdokpüspöki	Erdobénye
Amphora ovalis var. *libyca* (Ehr.) Cl.	–	1
Diploneis interrupta var. *heeri* (Pant.) Hust.	1	–
Epithemia subsalsa var. *validior* Pant.	–	3
Epithemia subsalsa Pant.	–	18
Fragilaria sp.	–	2
Melosira arenaria Moore var. *hungarica* Pant.	–	5
Melosira bituminosa var. *dilatata* Pant.	92	4
Melosira menilitica Pant.	–	20
Melosira sp.	–	5
Navicula bituminosa var. *robusta* Pant.	2	10
Navicula sp.	–	1
Nitzschia frustulum (Kütz.) Grun.	2	–
Rhopalodia sp.	–	3
Stephanodiscus minutus Pant.	–	24
Surirella sp.	3	–

Continued examination of stone-tool raw materials can contribute to determining their origins, particularly when they contain diatoms.

Acknowledgements

I am grateful to my colleagues in the Hungarian Geological Survey and the Hungarian Archaeological Institute who helped me during the research.

Literature Cited

BIRÓ, K. T. 1988. Distribution of lithic raw materials on prehistoric sites. Acta Arch. Acad. Sci. Hungarica 40:251–274.

HAJOS, M. 1959. Erdobénye-Ligetmajori kovafoldelofordulas. Magyar Allami Földtani Intezet Evi Jelentese 1955–56-rol:65–71.

———. 1968. Mátraalja miocén üledékeinek Diatomái. Geol. Hungarica Ser. Paleont. 37:1–401.

HEIN, J. R., D. M. SCHOLL, J. A. BARRON, M. J. JONES, AND J. MILLER. 1978. Diagenesis of late Genozoic diatomaceous deposits and formation of the bottom simulating reflector in the Southern Bering Sea. Sedimentology 25:155–181.

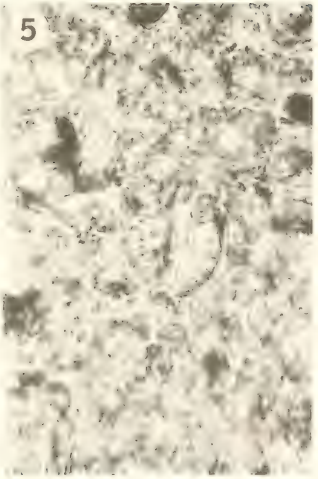
KOTLARCZYK, J. 1966. Pozium diatomowy z warstw krosnienskich na tle budowy geologiczny jednostki skolskiej w Karpatach polskich (Oligocen). Studium Geol. Polska 19:1–129.

Explanation of Plate

Plate 1, Figures 2–4

FIGURES 2–5. Limno-opalites of Erdobénye (thin sections). FIGURES 2–3. Scattered diatoms in opal matrix (× 160). FIGURE 4. *Melosira arenaria* var. *hungarica* Pant. (× 1000). FIGURE 5. *Epithemia subsalsa* Pant. (× 1000). Specimens identified from strewn slides.

1. 2.
3. 4.



Did Europeans Introduce *Asterionella formosa* Hassall to New Zealand?

by

Margaret A. Harper

Geology Department, R. S. E. S., Victoria University of Wellington,
P. O. Box 600, Wellington, New Zealand

with 1 table

Abstract: Evidence (dates and exotic pollen) from New Zealand lake cores indicates that *Asterionella formosa* Hassall, which became widespread during the period of European settlement, was not present in New Zealand earlier. This cannot be attributed to differential solution, as there is good preservation of diatoms in cores and *A. formosa* occurs in grab samples from lakes in which it is living at present. It is not due to changes in lake conditions, as earlier Polynesian settlers burnt forests, changing lake conditions without *A. formosa* appearing. *Asterionella formosa* has not been found in pre-European sediment anywhere in Australasia. This paper suggests some possible means for its introduction to the area by Europeans.

Introduction

An organism can be introduced into a given region only if it is capable of living there and the region was isolated from its previous distribution before introduction. *Asterionella formosa* Hassall is usually considered cosmopolitan (Foged 1979). Round (1984), however, noted that it does not survive high water temperatures and is generally absent from the tropics. Migrating waterfowl are capable of spreading *A. formosa* as viable cells occur in their guts, and cells can also survive for several days encased in any mud waterbirds may transport (Round 1984). New Zealand's freshwaters are a very long distance from any other temperate freshwaters except those of southern Australia and Tasmania. *Asterionella formosa* may be recently introduced to Australia as it has not been found there in cores, only in water samples (Bradbury 1986; Shiel et al. 1982; Bales et al. 1980). It also does not occur in the alpine lakes of New Guinea (Peterson 1976; Vyverman 1992), otherwise these could act as transmission points to Australia. The only migrant Australian waterfowl are black ducks and grey teal, which fly out to sea during severe droughts, and some reach New Zealand (Frith 1967). Most waterbirds found in New Zealand also occur in Australasia, some in Southeast Asia and the Indian Ocean, but only the seabirds have a worldwide distribution (Clements 1974). No seabirds would be likely to have reached New Zealand without feeding, washing, and defecating in the tropics or on the seashore (pers. comm. R. Hitchmough, Victoria University), which would cleanse them of *A. formosa*.

Asterionella formosa is widespread in New Zealand, being found in 64 out of 141 lakes for which there are phytoplankton records (Cassie 1988). Many of the lakes in which it has not been recorded are shallow, saline, or humic. It is most common in mesotrophic lakes, present in 72 % of those sampled, but is also found in oligotrophic (48 %) and eutrophic lakes (26 %).

Materials and Methods

The lakes chosen were those in which *A. formosa* had been recorded in the phytoplankton (Cassie 1988). Samples were taken from the New Zealand Oceanographic Institute's collection of cores from the South Island Lakes Pukaki (L389, L390, L391, L392), Taylor (L421), Sheppard (L423), Manapouri (L1104), and Te Anau (L1204 pt. 1–4 L1260 pt. 1), and from the North Island Lakes Taupo (L1133) and Waikaremoana (L1102). The Pukaki samples contained too few diatoms for use in this study. Other North Island samples came from Tutira (Land Resources core P4 and Victoria University of Wellington lake cores LT 9, 11, 14 and 16), Rotoiti (Waikato University RC 10 and 15), and from D. S. I. R. Water Sciences Division cores from Tarawera (B, C) and Okataina (D, E). B. Schakau and V. Stout of Canterbury University sent the author both South Island core and grab samples from Grasmere and grab samples from Camp, Clearwater, Emma, Horseshoe, Pearson, Sarah, Sheppard, and Taylor. Lowe and Green (1987) give morphometric details for all these lakes except Camp (max. depth 18 m) and Horseshoe (max. depth 17 m).

Samples were taken at intervals of 0.1 m or less downcore. The samples were treated with hydrogen peroxide and hydrochloric acid (Patrick and Reimer 1966), and sand was removed by sedimentation. Each sample was suspended in 15 ml of distilled water and a drop mounted on a circular 15 mm diameter coverslip. The circumference and a diameter transect were examined using × 480 and × 1200 magnification; in many cases more than one drop was examined so 1000–10,000 diatoms were seen except at the levels of storm events in Tutira cores.

Results

Asterionella formosa occurs in grab samples from Lakes Camp, Emma, Grasmere, Horseshoe, Pearson, Sarah, Sheppard, and Taylor, but not Clearwater. The occurrence of *A. formosa* in grab samples nearly matches that in planktic diatom records. Table 1 gives details of the core studies. *Asterionella formosa* was found only in the uppermost sediments in nine cores from seven lakes and was absent from all sediment in seven cores from five other lakes. In the six lakes in which a date for first appearance can be estimated, it is after 1880, with the doubtful exception of 1810 in one core from Lake Taupo, which is discussed below. *Asterionella formosa* occurs throughout Tutira lake cores LT 9, 11, 14; the sediment in these has all been deposited in this century, most of it in a few storms. In LT 16 it occurs only in the upper part, with *Pinus* pollen. Results from a lake core from Lake Rotorua come from Rawlence (1984) and from the south end of Lake Taupo from Rawlence and Reay (1976).

Discussion

Diatoms with thinner walls can be dissolved either in the water column or in the sediment, but the diatoms in the lake cores investigated here showed no signs of dissolution.

Asterionella formosa is found in grab samples in all the lakes except one where it occurs in planktic diatom records, indicating that it is not lost during sedimentation. The one

TABLE 1. Cores from lakes containing *Asterionella* and its first appearances.

	Asterionella in core?	Present from	Dating method	First planktic record	Time period (ky B.P.)
Rawlence's results					
Rotorua	+	1904	^{210}Pb	1966	0.12–0.01
Taupo (S.core)	+	1810?	^{210}Pb	1966	1.4–0.02
***Asterionella* content changes**					
Taupo (N. core)	+	1890s	Pinus	1966	post 0.2?
Rotoiti (RC 10)	+	1886	Tarawera	1969	1.8–0.01
Rotoiti (RC 15)	+	post 1886	Tarawera	1969	0.7–0.02
Grasmere	+*	1890s	Pinus	1972	5.6–0.02
Waikaremoana	+	?	?	1978	? (0.4 m)
Okataina (core E)	+	post 1886	Tarawera	1972	1.8–0.02
Tutira (LT16)	+	1890s	Pinus	1975	post 1.8
Cores without *Asterionella*					
Okataina (core D)	0	post 1886	Tarawera	1972	0.7–0.05
Tarawera (core C)	0	post 1886	Tarawera	1974	0.15–0.05
Tarawera (core B)	0	post 1886	Tarawera	1974	0.7–0.02
Te Anau (1260)	0	?	natives	1975	3–0.05?
Te Anau (1204)	0	?	?	1975	6–0.05?
Taylor	0*	?	^{14}C, natives	1960	6.0–5.0
Sheppard	0*	?	(no pollen)	1975	? (1.9 m)
Manapouri	0	?	(no pollen)	1975	? (2.0 m)
Tutira(P4)	0	?	^{14}C, tephras	1975	5.4–1.0
***Asterionella* at all levels**					
Tutira (LT14)	+	1910s?	storm events	1975	post 0.04
Tutira (LT11)	+	1890s?	storm events	1975	post 0.1?
Tutira (LT9)	+	1940s?	storm events	1975	post 0.01

+ = A. formosa present, *= A. formosa in grab sample, 0 = no A. formosa in core. ^{210}Pb = lead isotype dating, Pinus = exotic Pinus sp. pollen present, Tarawera = Tarawera tephra erupted in AD 1886, natives = native pollen only. Parentheses in the first column indicate which in the last column indicate the length of core examined. Planktic records are from Cassie (1988) and references therein.

exception was of Lake Clearwater, where the grab sample was dominated by benthic diatoms showing a strong shoreline influence, despite being taken from 17 m. Preservation was excellent in most samples, as was indicated by the occurrence of fragile, thin-walled *Rhizosolenia* sp. in the Rotoiti core at nearly all levels down to the base of the core, which was at the top of the Taupo pumice from the 1850 y B.P. eruption of Taupo (pers. comm. C. Nelson, Earth Sciences, Waikato University). Many of the North Island lakes contain volcanic glass shards that protect diatom frustules from being dissolved.

Table 1 shows that *A. formosa* only occurs late in the sediment record or, in several lakes, in the recent uncompacted sediment that escapes the corer. The time periods covered by the cores include, in several cases, the period of extensive moa grazing (pre 1.0 ky B.P.),

and that of Maori forest burning (1.0–0.1 ky B.P.), and many pre-European falls of volcanic ash into North Island lakes. *Asterionella formosa* did not appear in any of the cores as the result of these habitat changes. The author has previously examined in less detail cores with planktic diatom rich (> 50 % of diatom population and > 200 diatoms per count) intervals from the Rotorua basin (2–4, 6–8, 20–25 ky B. P), from Waiatarua in Auckland (6–7 ky B. P.), and Maratoto (9–12 ky B. P.), and none of these contain *A. formosa*.

The earliest known European introduction to New Zealand water was watercress seed in 1840 (Howard-Williams et al. 1987). The first introduction of fish was of Atlantic salmon ova in 1864, but these died (McDowall 1987). Sometimes doubtful ova were dumped in local waters in hopes that some might survive. In 1852 salmon ova had been introduced to Tasmania, also unsuccessfully. There is no proof that living diatoms could not coexist with dead ova. Further ova sent to Tasmania in 1866 lived, and in 1868 ova from these salmon were sent to New Zealand; they also lived and were bred from. Proof that other organisms were introduced with ova comes from the appearance of *Elodea canadensis* with ova introduced in 1868 (Howard-Williams et al. 1987). Ova were kept in a double container, the inner perforated. The water in the outer container was renewed at intervals and the whole kept cool in an ice house. Other fish and ova were introduced from 1868 on, including carp, trout, whitefish, and perch. Once *A. formosa* was introduced to either Australia or New Zealand it could be spread by ducks.

Asterionella formosa is absent from the pre-European settlement samples examined either because it did not then occur in New Zealand or because a lack of specific nutrients restricted its growth to a few special environments. Round (1984) notes the suggestion that it is associated with faecal input to lakes. Prior to European settlement the major grazers were moas (ratite birds), which became extinct soon after the arrival of the first Polynesian settlers about 1000 y B. P. Moa remains have been found near lakes Taylor and Sheppard, the cores from which contain no *A. formosa*. It is only possible to examine a small proportion of the diatom populations that are present in lake sediments, but consistent absence of *A. formosa* in pre-European sediments is as clearly shown as in most biostratigraphy.

The earliest date for the first appearance of *A. formosa* is 1810 (Rawlence and Reay 1976), for the South core from Lake Taupo. This precedes any known introduction of water organisms. The date is derived from ^{210}Pb measurements, but it is open to doubt. The North core, which contains occasional *A. formosa* to 0.3 m downcore has *Pinus* pollen present below that, at 0.35 m. *Pinus* was definitely introduced to New Zealand by Europeans. In the South core the 70–80 mm downcore sample contains twice as much unsupported ^{210}Pb as the 60–70 mm sample (McCabe and Ditchburn 1976), indicating slumping.

It is just possible that *A. formosa* was always present, but in such minute populations that it has not been found in cores, and that its growth is stimulated by mammalian faeces. These were sparse in New Zealand before the introduction of grazing animals. Lakes Waikaremoana and Okataina have catchments of native forest, so are not affected by European farming, but faecal matter could come from feral pigs, goats, possums, and deer introduced by Europeans from the 1770s on (Beaglehole 1974). Examination of Australian cores would test this possibility; that country has many native mammals.

Conclusion

Occurrence of *A. formosa* in recent New Zealand lake sediments indicates European influence. Europeans could have introduced this diatom and others with fish or fish ova in the 1860s. The alternative hypothesis is that New Zealand was lacking mammalian grazers whose faeces provide an important source of nutrients for the growth of *A. formosa*.

Acknowledgements

The author thanks the following for their help with this project: R. Walcott for use of facilities, P. Froggatt for advice on tephras, and W. McLea for pollen identifications at the Geology Dept., Victoria University, Wellington, N. Z.; J. Irwin and R. Pickrill for samples from lake cores held by the New Zealand Oceanographic Institute; C. Nelson and D. Lowe of the School of Earth Sciences, Waikato University, Hamilton, N. Z. for samples and information from a Lake Rotoiti core; V. Stout and B. Schakau of the Department of Zoology, Canterbury University, Christchurch, N. Z. for grab samples and for samples and information from a Lake Grasmere core; D. Eden and M. Page of D.S.I.R. Land Resources, Palmerston North, N. Z. for samples and information from a Lake Tutira swamp core; G. Turner of the Department of Physics, Victoria University, for samples and information from Lake Tutira lake cores; N. Kennedy of Land Resources, Rotorua, for samples and information on cores from the Rotorua basin; M. McGlone of Land Resources, Lincoln, R. Newnham of Auckland University for samples and information on a core from Waiatarua, Auckland; J. Green of Waikato University for samples and information on a core from Maratoto; and to S. Stein and D. Jurdy of the Department of Geological Sciences, Northwestern University, Evanston, Illinois, U. S. A. for facilities and help with completing this paper.

Literature Cited

Bales, J. L., G. K. Curtin, I. C. Campbell, and B. T. Hart. 1980. Eutrophication study of Lake Daylesford, Victoria. Aust. J. Mar. Freshw. Res. 31:573–587.

Beaglehole, J. C. 1974. Life of Captain Cook. Stanford University Press, California. 804 pp.

Bradbury, J. P. 1986. Late Pleistocene and Holocene Paleolimnology of Two Mountain Lakes in Western Tasmania. Palaios 1:381–388.

Cassie, V. 1988. Checklist of New Zealand Diatoms. Bibl. Diatomologica 4:1–129.

Clements, J. F. 1974. Birds of the World, a check list. Two Continents Publishing Group, New York, 521 pp.

Foged, N. I. 1979. Diatoms in New Zealand. Bibl. Phycologica 47:1–225.

Frith, H. J. 1967. Waterfowl in Australia. East West Center Press, Hawaii, 328 pp.

Howard-Williams, C., J. S. Clayton, and I. M. Johnstone. 1987. Macrophyte invasion. Pp. 307–331 *in* Inland Waters of New Zealand, A. B. Viner, ed. Government Printer, Wellington.

Lowe, D. J. and J. D. Green. 1987. Appendix A. Pp. 460–474 *in* Inland Waters of New Zealand, A. B. Viner, ed. Government Printer, Wellington.

McCabe, W. J. and R. G. Ditchburn. 1976. Sedimentation rates measured by Lead-210 method on a Lake Taupo core. Inst. Nuclear Sci. Contr. 782:1–5. D. S. I. R. Lower Hutt, New Zealand.

McDOWALL, R. M. 1987. Impacts of exotic fishes on the native fauna. Pp. 333–347 *in* Inland Waters of New Zealand, A. B. Viner, ed. Government Printer, Wellington.

PATRICK, R. AND C. W. REIMER. 1966. Diatoms of the United States. Vol. 1. Monograph No. 13, Acad. Nat. Sci., Philadelphia. 688 pp.

PETERSON, J. A. 1976. The Lakes. Pp. 93–112 *in* The Equatorial Glaciers of New Guinea, G. S. Hope, J. A. Peterson, U. Radok and I. Allison, eds. A. A. Balkema, Rotterdam.

RAWLENCE, D. J. 1984. A study of the pigment and diatoms in a core from Lake Rotorua, North Island, New Zealand, with an emphasis on recent history. J. R. Soc. N. Z. 14:119–132.

RAWLENCE, D. J. AND P. F. REAY. 1976. Diatom numbers and phosphorus levels in deepwater sediment from Lake Taupo, New Zealand. N. Z. J. Mar. Freshw. Res. 10:589–595.

ROUND, F. E. 1984. The Ecology of the Algae. Cambridge University Press, Cambridge. 653 pp.

SHIEL, R. J., K. F. WALKER, AND W. D. WILLIAMS. 1982. Plankton of the lower River Murray, South Australia. Aust. J. Mar. Freshw. Res. 33:301–327.

VYVERMAN, W. 1992. Altitudinal distribution of non-cosmopolitan desmids and diatoms in Papua New Guinea. Br. Phycol. J. 27:49-63.

The Biochronology of Freshwater Planktonic Diatom Communities in Western North America

by

William N. Krebs

Amoco Production Company, 550 Westlake Park Blvd.,
Houston, Texas 77079

with 2 figures

Abstract: The oldest known freshwater diatoms in North America are middle Eocene in age. During the Tertiary, there have been four distinct planktonic diatom communities in temperate freshwater lakes of western North America: (1) *Aulacoseira*-pennate genera (Eocene-Oligocene), (2) *Actinocyclus-Thalassiosira-Aulacoseira* (early to middle Miocene), (3) *Mesodictyon-Cyclotella-Aulacoseira* (late Miocene), (4) *Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira* (Pliocene-Holocene). The *Actinocyclus-Thalassiosira* community may have had a marine or brackish water origin; its appearance during the early Miocene coincided with species radiations of both genera in marine waters, high stands of sea level, and the formation of lake basins by volcanism and extensional tectonics. Freshwater planktonic and marine diatom turnovers during the Neogene occurred during major low stands of sea level, and may be related to oceanographic-climatic change, environmental stress, and species competition. The modern centric diatom community found in temperate freshwater lakes worldwide (*Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira*) has a short geologic history in North America (ca. 6 Ma) compared to the long geologic range of freshwater diatoms (ca. 45 Ma). The timing and order of first occurrences of freshwater centric planktonic diatom genera in marine and lacustrine rocks are very similar.

Introduction

Interesting articles dealing with the origin and evolution of freshwater diatoms have appeared in the recent past (e.g., Round and Sims 1981). Unfortunately, knowledge of the fossil record of freshwater diatoms has been sketchy at best, and there have been few efforts at synthesis of the known data. As a result, discussions of freshwater diatom evolution have relied heavily upon morphology and ecology and have not benefitted from the actual recorded geologic history of freshwater diatoms. Recently, however, workers from several continents have presented biochronologies of freshwater diatoms from different areas (Servant-Vildary 1978; Gasse 1980; Bradbury and Krebs 1982; Khursevich 1982, 1990; Loginova 1982; Loginova et al. 1984; Van Landingham 1985; Krebs et al. 1987; Fourtanier and Gasse 1988; Kociolek and Stoermer 1989), and there have even been worldwide comparisons (Fourtanier 1987; Serieyssol 1988). Although there are problems with such comparisons (taxonomy, age dating, and contamination), a few general patterns

of freshwater diatom biochronology have emerged (Fountanier 1987). Future speculation on the evolution of freshwater diatoms should therefore benefit from increased knowledge of their fossil record. The purpose of this paper is to document the succession of freshwater planktonic diatom communities during the Tertiary in western North America and to speculate on the factors that may have been responsible for these turnovers.

Materials and Methods

The hundreds of samples of lacustrine diatomaceous sediment collected for this study came from over 100 sites in western North America. Most samples are outcrop material, and the majority of them came from the Great Basin of the United States. A few are subsurface well samples. Neogene and Quaternary material is from localities listed in Appendix 1; Paleogene localities are listed in Appendix 2. In addition, Lohman and Andrews (1968) have described a late Eocene diatom assemblage from Wyoming. All samples were disaggregated with acids and the residue made into strewn slides using a permanent mounting medium (e.g., Hyrax). The slides were then scanned with a Leitz Orthomat light microscope.

Fortunately, many lacustrine diatomaceous deposits in western North America are associated with volcanic rock and/or fossil mammals. In many cases, the volcanic rock has been radiometrically dated or the fossil mammals have furnished a relative geologic age for an outcrop. By these means, many of the deposits have been dated independently of their fossil diatom content, thereby permitting their fossil floras to be stacked in geochronological order (Krebs et al. 1987; Krebs and Bradbury, in prep.). Constituent genera and species can be traced through geologic time, thus documenting the biochronology of freshwater diatoms.

In this study, only planktonic genera common to temperate freshwater (low conductivity) permanent bodies of water are considered. Diatoms characteristic of saline lakes and ephemeral aquatic environments have been excluded. The word community is herein used to mean a recurrent association characteristic of a particular habitat, e.g., *Stephanodiscus* and *Cyclotella* in theopen wateps of a temperate freshwater lake, concurrently or at different times.

Results

The results of this study are depicted in Figure 1. In western North America during the Tertiary, there have been four distinct diatom communities that have occupied the plankton of temperate freshwater lakes: (1) *Aulacoseira*-pennate genera (e.g., *Fragilaria*), (2) *Actanocyclus-Thalassiosira-Aulacoseira*, (3) *Mesodictyon-Cyclotella-Aulacoseira*, and (4) *Stephanodiscus-Cyclotella-Cyclostephanos Aulacoseira.*

The most ancient community, *Aulacoseira*-pennate genera, is at least as old as middle Eocene (e.g., the Dewey Beds of Idaho) (Leonard and Marvin 1982). It was the sole planktonic diatom community in temperate freshwater lakes during the Paleogene and can still be found in some North American lakes of today. The second planktonic diatom community, *Actinocyclus-Thalassiosira-Aulacoseira*, is first recorded in North America from the early Miocene of western Nevada (Copper Kettle Canyon, Churchill Co., Nevada). Oligocene samples from Nevada and Colorado, and Oligocene-earliest Miocene samples from southwestern Montana contain neither *Actinocyclus* nor *Thalassiosira.* This community, however, may have existed earlier during the early Miocene or even late Oligocene, but because of the scarcity of samples of these ages, there is no record as yet of these genera at those times. An any case, the *Actinocyclus-Thalassiosira-Aulacoseira* community

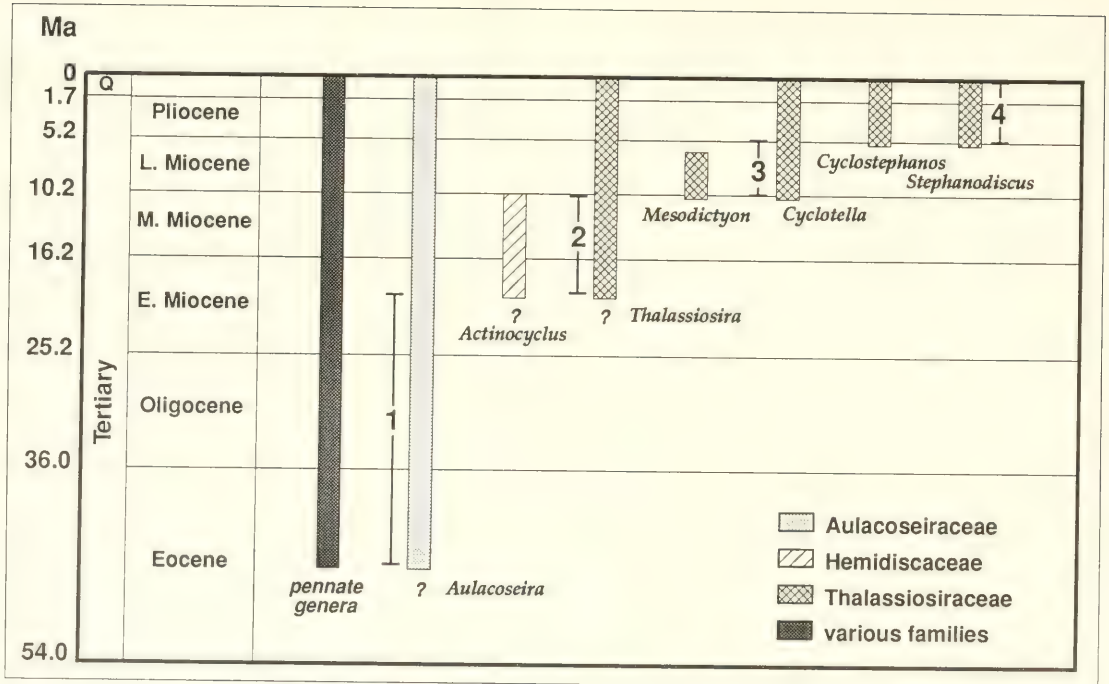


FIGURE 1. Geologic ranges of freshwater planktonic diatom genera in North America. Numbers refer to different planktonic diatom communities.

existed as early as ca.19 Ma and was the characteristic planktonic diatom association of North American temperate freshwater lakes through the end of the middle Miocene (ca. 10 Ma).

During the latest middle Miocene (ca. 11 Ma), and in association with *Actinocyclus-Thalassiosira-Aulacoseira*, the first species of *Cyclotella* and *Mesodictyon* appeared. This third community, *Mesodictyon-Cyclotella-Aulacoseira*, replaced the *Actinocyclus-Thalassiosira-Aulacoseira* association by the beginning of the late Miocene (10.2 Ma), and persisted into the late late Miocene (< 7 Ma) in North America. An fact, the transition from this association to the fourth community, *Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira* probably occurred during the Messinian (latest Miocene) in North America. Unfortunately, there are very few freshwater lacustrine diatomaceous deposits of that age in North America. *Stephanodiscus* has been found in Messinian age rocks elsewhere in the world (Schrader and Gersonde 1972; Fourtanier 1987).

The modern community of *Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira*, so characteristic of temperate freshwater lakes, was widespread and diversified in North America during the earliest Pliocene. Although many species extinctions of these genera have occurred during the last 5 Ma, Pliocene-Pleistocene floras have a remarkably modern appearance in comparison to the older freshwater planktonic diatom communities. In fact, some species may be relatively long-lived (e.g., *Stephanodiscus astrea*, *Cyclotella pseudostelligera*), and as a consequence, paleoecologic interpretations of these floras are more precise.

Discussion

Aulacoseira is clearly a very ancient and successful freshwater genus, possibly having evolved from the Eocene-Oligocene marine genus *Strangulonema* (Round et al. 1990). In North America, the earliest occurrence of *Aulacoseira* is in the middle Eocene, and in marine rocks worldwide, it is the oldest known, exclusively freshwater genus, noted in sections as old as late Eocene (Schrader 1977; Fenner 1981) (Fig. 2). In fact, the first occurrence of the other exclusively (or as with *Cyclotella*, nearly exclusively) freshwater centric planktonic genera in marine rocks is very similar in order and timing to first occurrences in the lacustrine record. For example, *Cyclotella* has definitely been found in Lower Upper Miocene marine rock (Fourtanier 1987), and it may occur in the marine Temblor Formation (Hanna 1932) of latest early-earliest middle Miocene age, although there is doubt as to the generic affinities of this species (*C. kellogii*) (E. Theriot, pers. comm.). *Mesodictyon* and *Stephanodiscus* have been reported by Fourtanier (1987) in Lower Upper Miocene and Upper Upper Miocene sections, respectively, of the same core taken from offshore Angola. At a different core site in offshore Angola, Fourtanier (1987) also reported the possible occurrence of *Cyclostephanos* in the Upper Upper Miocene. This similarity between the marine and freshwater records suggests that the diatom biochronology presented here may have worldwide significance.

Although it is not yet possible to explain the succession of these four different freshwater diatom communities through the Tertiary, there are some interesting events in the marine realm that may have had an impact. For example, both marine *Actinocyclus* and *Thalassiosira* appear to have experienced species radiations during the latest Oligocene and early Miocene (Radionova 1987, 1990; J. A. Barron and N. I. Strelnikova, pers. comm.), about the same time that both genera appear in the North American lacustrine record. The early Miocene was a period of high sea level relative to that of today (Haq et al. 1987), in fact, the highest sea level of any time in the Neogene or Quaternary. During the early Miocene (ca. 17 Ma), the first episode of basin-and-range tectonics occurred (Stewart and

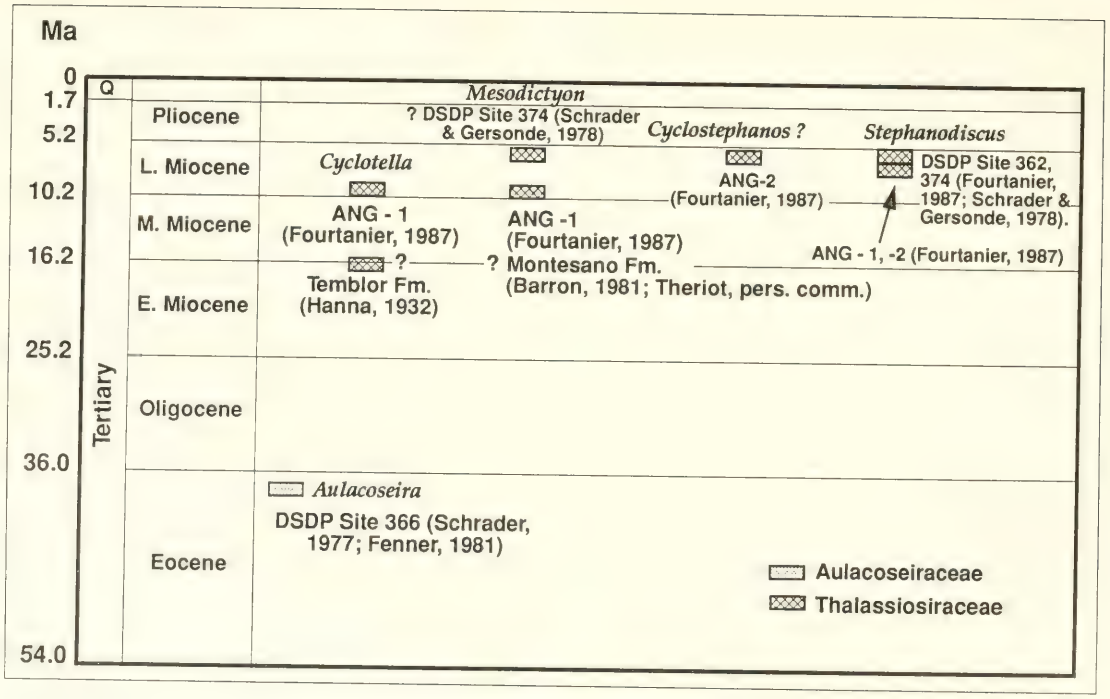


FIGURE 2. Earliest known occurrences of freshwater planktonic diatom genera in marine sediments.

Carlson 1976), creating many large lake basins and coinciding with the formation of California marine basins in which the Monterey and Sisquoc Formations accumulated (Crouch 1979; Ingle 1980, 1981). This simultaneous event probably explains why most of the lacustrine diatomite of the Great Basin is of the same age range as the marine diatomites of the California coast. In addition, extensive basaltic volcanism during the Miocene may have dammed drainage patterns and created lakes (Axelrod 1956; Smiley and Rember 1985). Both *Actinocyclus* and *Thalassiosira* might easily have been introduced through estuaries, rivers, and by birds into the newly formed early Miocene lakes of the western United States. It is interesting to note that both genera today have species that are euryhaline (Hasle 1977, 1985). Freshwater planktonic diatom community turnovers at ca. 10.5 Ma and ca. 5.5 Ma coincide with major sea level regressions and turnovers of marine diatoms (Radionova 1990). These regressions are believed to have been caused by major pulses of antarctic glaciation that affected the world's oceans and climatic patterns, producing increased aridity on several continents (Janecek and Rea 1983; Stein and Robert 1985; Woodruff 1985; Bloomstine and Rea 1986; Rea and Bloomstine 1986; Stein 1986; Pickford 1987). The lakes of the world at those times must have been affected by changes in their distribution, sizes, chemistry, and seasonal structure, all affecting their diatom phytoplankton. This severe environmental stress may have led to extinctions and the rapid evolution of new species and genera capable of out-competing older freshwater planktonic diatoms. In any case, it is clear that the modern diatom community found in temperate freshwater lakes of North America and elsewhere (*Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira*) is of recent origin (ca. 6 Ma) compared to the long geologic history of freshwater diatoms (ca. 45 Ma).

Conclusions

(1) The oldest known freshwater diatoms in North America are middle Eocene (ca. 45 Ma) in age.

(2) In western North America, there have been four distinct temperate freshwater planktonic diatom communities during the Tertiary: (1) *Aulacoseira*-pennate genera (Eocene-Oligocene); (2) *Actinocyclus-Thalassiosira-Aulacoseira* (early and middle Miocene); (3) *Mesodictyon-Cyclotella-Aulacoseira* (late Miocene); (4) *Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira* (Pliocene-Holocene).

(3) The origin of obligate freshwater *Actinocyclus* and *Thalassiosira* during the early Miocene coincided with species radiations of both genera in marine waters, high stands of sea level, and the creation of lake basins by volcanism and extensional tectonics.

(4) The *Actinocyclus-Thalassiosira* community may have had a marine or brackish water origin.

(5) Freshwater planktonic diatom community turnovers during the Neogene at ca. 5.5 Ma and ca. 10.5 Ma coincided with major sea level regressions and turnovers in marine diatoms. These regressions may have been related to major oceanographic and climatic changes that induced environmental stress, rapid diatom evolution, and subsequent species competition.

(6) The nearly synchronous formation of marine diatomites in California (e.g., the Monterey and Sisquoc Formations) and lacustrine diatomites in the Great Basin is related to tectonism that simultaneously produced both onshore and offshore basins.

(7) The modern diatom community that dominates freshwater temperate lakes of North America (*Stephanodiscus-Cyclotella-Cyclostephanos-Aulacoseira*) has a short geologic history (ca. 6 Ma) relative to the long geologic range of freshwater diatoms (ca. 45 Ma).

(8) The order and timing of first occurrences of freshwater planktonic centric diatom genera (e.g., *Aulacoseira, Mesodictyon, Cyclotella, Cyclostephanos, Stephanodiscus*) in marine and lacustrine rocks are similar.

Acknowledgements

The author thanks J. Platt Bradbury, Elisabeth Fourtanier, Edward Theriot, John Barron, Howard Schorn, and John Stewart for many informative and stimulating discussions.

Literature Cited

AXELROD, D. I. 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Pub. Geol. Sci. 33:1–321.

———. 1958. The Pliocene Verdi flora of western Nevada. Univ. Calif. Pub. Geol. Sci. 34:91–159.

BARRON, J. A. 1981. Marine diatom biostratigraphy of the Montesano Formation near Aberdeen, Washington. Geol. Soc. Amer. Spec. Pap. 184:113–125.

BLOOMSTINE, M. K. AND D. K. REA. 1986. Post-Middle Oligocene eolian deposition from the trade winds of the southeast Pacific. Init. Repts. Deep Sea Drilling Proj. 92:331–340.

BRADBURY, J. P. AND W. N. KREBS. 1982. Neogene and Quaternary lacustrine diatoms of the western Snake River Basin, Idaho-Oregon, U. S. A. Acta. Geol. Acad. Sci. Hungar. 25:97–122.

CROUCH, J. K. 1979. Neogene tectonic evolution of the California continental borderland and western Transverse Ranges. Geol. Soc. Amer. Bull. 90:338–345.

FENNER, J. 1981. Diatoms in the Eocene and Oligocene sediments off NW Africa. Their stratigraphic and paleogeographic occurrences. Ph.D. dissert. Kiel, Germany. 230 pp.

FIRBY, J. R. 1973. An Oligocene non-marine molluscan fauna from eastern Nevada. Jour. Paleontol. 47:115–120.

FOURTANIER, E. 1987. Diatomées Néogenes d'Afrique: approche biostratigraphique en milieux marin (sud-ouest africain) et continental. Ph.D. dissert., Ecole Normale Supérieure de Fonteney Saint-Cloud, France. 365 pp.

FOURTANIER, E. AND F. GASSE. 1988. Premiers jalons d'une biostratigraphie et évolution des diatomées lacustres d'Afrique depuis 11 Ma. C. R. Acad. Sci. Paris 306:1401–1408.

GASSE, F. 1980. Les diatomées lacustres plio-pléistocenes du Gadeb (Éthiopie): systématique, paléoécologie, biostratigraphie. Rev. Algol., Mem. Ser. 3:1–249.

HAQ, B. U., J. HARDENBOL, AND P. R. VAIL. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235:1156–1167.

HANNA, G. D. 1932. The diatoms of Sharkstooth Hill, Kern County, California. Proc. Calif. Acad. Sci. 20:161–263.

HASLE, G. R. 1977. Morphology and taxonomy of *Actinocyclus normanii* f. *subsalsa* (Bacillariophyceae). Phycologia 16:321–328.

———. 1985. *Thalassiosiropsis*, a new diatom genus from the fossil records. Micropaleontology 31:82–91.

INGLE, J. C., Jr. 1980. Cenozoic paleobathymetry and depositional history of selected sequences within the southern California continental borderland. *In* Studies in Micropaleontology, W. V. Sliter, ed. Cushman Found. Foram. Res. Spec. Pub. 19:163–195.

———. 1981. Origin of Neogene diatomites around the North Pacific rim. Pp. 117–132 *in* The Monterey Formation and Related Siliceous Rocks of California, R. E. Garrison, R. G. Douglas, K. E. Pisciotto, C. M. Isaacs, and J. C. Ingle Jr., eds. Soc. Econ. Paleo. Mineral. Pac. Sect. Spec. Pub.

JANECEK, T. R. AND D. K. REA. 1983. Eolian deposition in the northeast Pacific Ocean: Cenozoic history of atmospheric circulation. Geol. Soc. Amer. Bull. 94:730–738.

KHURSEVICH, G. K. 1982. Neogene diatom assemblages from Byelorussia and their stratigraphic significance. Acta. Geol. Acad. Sci. Hungar. 25:123–134.

———. 1990. Evolution and phylogeny of some diatom genera of the class Centrophyceae. Pg. 54 *in* Abstracts of the 11th International Symposium on Living and Fossil Diatoms, San Francisco, August 13–17.

KOCIOLEK, J. P. AND E. F. STOERMER. 1989. Phylogenetic relationships and evolutionary history of the diatom genus *Gomphoneis*. Phycologia 28:438–454.

KONIZESKI, R. L. 1961. Paleoecology of an early Oligocene biota from Douglass Creek Basin, Montana. Geol. Soc. Amer. Bull. 72:1633–1642.

KREBS, W. N. , J. P. BRADBURY, AND E. C. THERIOT. 1987. Neogene and Quaternary lacustrine diatom biochronology, western U. S. A. Palaios 2:505–513.

KREBS, W. N. AND J. P. BRADBURY. In Press. Geologic ranges of lacustrine *Actinocyclus* species, western U. S. A. U.S. Geol. Surv. Prof. Pap.

LOHMAN, K. E. AND G. W. ANDREWS. 1968. Late Eocene nonmarine diatoms from the Beaver Divide area, Fremont County, Wyoming. U. S. Geol. Surv. Prof. Pap. 593–E:1–26.

LEONARD, B. F. AND R. F. MARVIN. 1982. Temporal evolution of the Thunder Mountain Caldera and related features, central Idaho. *In* Cenozoic Geology of Idaho, W. Bonnichsen and R. M. Breckenridge, eds. Idaho Bur. Mines Geol. Bull. 26:23–42.

LOGINOVA, L. P. 1982. The Likhvin diatom flora from the central part of the East-European Plain, its paleogeographical and stratigraphical significance. Acta. Geol. Acad. Sci. Hungar. 25:149–160.

LOGINOVA, L. P., E. G. LUPIKINA, AND G. K. KHURSEVICH. 1984. Sur une nouvelle espèce de *Cyclostephanos* Round et sur sa signification stratigraphique. Rapps. Acad. Sci. Bieloruss. 28:170–173.

MACGINNITIE, H. D. 1953. Fossil plants of the Florissant beds, Colorado. Contr. Paleo. Carnegie Inst. Wash. Pub. 599:1–198.

PICKFORD, M. 1987. Concordance entre la paléontologie continentale de d'Est africain et les événements paléo-oceanographique au néogene. C. R. Acad. Sci. Paris 304:675–678.

RADIONOVA, E. P. 1987. Diatom morphology of the genus *Cestodiscus* from lower middle Miocene deposits of the tropical zone of the Pacific Ocean. Acad. Sci., U. S. S. R., Instit. Geol., Micropaleo. Edit. 29:141–154.

———. 1990. Structure of the Neogene diatom assemblage of the tropical Pacific. Pg. 90 *in* Abstracts of the 11th International Symposium on Living and Fossil Diatoms, San Francisco, Aug. 13–17.

REA, D. K. AND M. K. BLOOMSTINE. 1986. Neogene history of the South Pacific trade winds: evidence for hemispherical asymmetry of atmospheric circulation. Paleogeog. Paleoclimat. Paleoecol. 55:55–64.

ROUND, F. E. AND P. A. SIMS. 1981. The distribution of diatom genera in marine and freshwater environments and some evolutionary considerations. Pp. 301–320 *in* Proceedings of the 6th International Symposium on Recent and Fossil Diatoms, R. Ross, ed. O. Koeltz, Koenigstein.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The Diatoms. Biology and Morphology of the Genera. Cambridge Univ. Press, Cambridge. 747 pp.

SCHRADER, J. H. 1977. Diatoms in DSDP leg 41 sites. Init. Repts. Deep Sea Drilling Proj. 41:791–811.

SCHRADER, H. J. AND R. GERSONDE. 1972. The late Messinian Mediterranean brackish to freshwater environment, diatom floral evidence. Init. Repts. Deep Sea Drilling Proj. 42:761–775.

SERIEYSSOL, K. K. 1988. Biostratigraphy and taxonomic interpretations based on the survey of fossil freshwater centric genera. Pg. 114 *in* Abstracts of the 10th International Symposium on Living and Fossil Diatoms, Joensuu, Finland, Aug. 28–Sept. 2, 1988.

SERVANT-VILDARY, S. 1978. Etude des diatomées et paléolimnologie du bassin Tchadien au Cénozoique supérieur: Travaux Doc. ORSTOM 84 (2 vols.). 346 pp.

SMILEY, C. J. AND W. C. REMBER. 1985. Physical setting of the Miocene Clarkia fossil beds, northern Idaho. Pp. 11–31 *in* Late Cenozoic history of the Pacific Northwest, C. J. Smiley, ed. Pacific Div. Amer. Assoc. Adv. Sci., San Francisco, California.

STEIN, R. 1986. Late Neogene evolution of paleoclimate and paleoceanic circulation in the northern and southern hemisphere—a comparison. Geol. Rundschau 75:125–138.

STEIN, R. AND C. ROBERT. 1985. Siliciclastic sediments at sites 588, 590, and 591: Neogene and Paleogene evolution in the southwest Pacific and Australian climate. Init. Repts. Deep Sea Drilling Proj. 90:1437–1455.

STEWART, J. H. AND J. E. CARLSON. 1976. Cenozoic rocks of Nevada—Four maps and brief description of distribution, lithology, age, and centers of volcanism. Nev. Bur. Mines Geol., map 52: 1–5.

VANLANDINGHAM, S. L. 1985. Potential Neogene diagnostic diatoms from the western Snake River Basin, Idaho and Oregon. Micropaleontology 31:167–174.

WILSON, M. V. H. 1980. Eocene lake environments: depth and distance—from shore variation in fish, insect, and plant assemblages. Paleogeog. Paleoclimat. Paleoecol. 32:21–44.

WOODRUFF, F. 1985. Changes in Miocene deep-sea benthic foraminferal distribution in the Pacific Ocean: relationship to paleoceanography. *In* The Miocene ocean:

paleoceanography and biogeography, J. P. Kennett, ed. Geo. Soc. Amer. Mem. 163:131–175.

Appendix 1. Neogene and Quaternary Diatom Sample Localities

1. Aldrich Station (?) Fm., east Walker River, 38.84°N, 119.06°W, Lyon Co., Nevada.
2. Alturas Fm., Howards Gulch, sec. 27, T42N, R15E, Modoc Co., California.
3. Alturas Fm., 3.5 miles west of Alturas, California Academy of Sciences Diatom Locality 36805, Modoc Co., California.
4. Augusta Mountains, unnamed unit, sec. 31, T24N, R39E, Churchill Co., Nevada.
5. Bruneau Fm., W. Snake River Plain, sec. 27, T5S, R4E, Elmore Co., Idaho.
6. Buffalo Canyon Fm., Buffalo Canyon, sec. 2, T15N, R37E, Churchill Co., Nevada.
7. Bully Creek Fm., type section, Harper Basin, sec. 11, T19S, R41E, Malheur Co., Oregon.
8. Chalk Hills Fm., base of formation, West Browns Creek, sec. 2, T5S, R1W, Owyhee Co., Idaho.
9. Chalk Hills Fm., Castle Creek, sec. 9, T6S, R1E, Owyhee Co., Idaho.
10. Chalk Hills Fm., Chalk Hills, sec. 20, T7S, R4E, Owyhee Co., Idaho.
11. Chalk Hills Fm., Shoofly Creek, lower Horse Hill ash, sec. 9, T7S, R3E, Owyhee Co., Idaho.
12. Chalk Hills Fm., type section, lower Horse Hill ash, sec. 25, T7S, R4E, Owyhee Co., Idaho.
13. Clarkia Basin, unnamed unit, sec. 13, T42N, R1E, Shoshone Co., Idaho.
14. Kelseyville Fm., Clear Lake, sec. 27, T13N, R9W, Lake Co., California.
15. Coal Valley Fm., Pine Grove Hill, sec. 2, T9N, R26E, Lyon Co., Nevada.
16. Copper Kettle Canyon, unnamed unit, sec. 26, T24N, R34E, Churchill Co., Nevada.
17. Turner Creek, unnamed unit, sec. 1, T41N, R8E, Modoc Co., California.
18. Dead Camel Mountains, unnamed unit, sec. 24, T18N, R26E, Churchill Co., Nevada.
19. Amoco Delta Stephan Szot No. 1 well, sec. 19, T14N, R1E, Cache Co., Utah.
20. Esmeralda Fm., "Diatomite Ridge," Stewart Valley, 38°37'02"N, 117°56'35"W, Mineral Co., Nevada.
21. Clarkia Basin, Emerald Creek, sec. 33, T43N, R1E, Benewah Co., Idaho.
22. Esmeralda Fm., Cedar Mountain, 38.5°N, 44.75°W, Mineral Co., Nevada.
23. Glenns Ferry Fm., Hagermen horse quarry, sec. 16, T7S, R13E, Twin Falls Co., Idaho.
24. Glenns Ferry Fm., sec. 1, T6S, R8E, Owyhee Co., Idaho.
25. Glenns Ferry Fm., Shoofly Creek, sec. 6, T7S, R3E, Owyhee Co., Idaho.
26. Glenns Ferry (?) Fm., Weiser, sec. 35, T15S, R46E, Washington Co., Idaho.

27. Goose Creek, unnamed unit, sec. 29, T8S, R43E, Baker Co., Oregon.
28. Michel T. Halbouty Federal No. 1 well, sec. 14, T17N, R28E, Churchill Co., Nevada.
29. Alturas Fm., Howards Gulch, sec. 22, T42N, R9E, Modoc Co., California.
30. Humboldt Fm., sec. 31, T31N, R52E, Eureka Co., Nevada.
31. IW-24, IW-26, Idaho Group, sec. 34, T12N, R4W, Washington Co., Idaho.
32. Juliaetta, unnamed unit, sec. 20, T37N, R3W, Nez Perce Co., Idaho.
33. Jungle Point, unnamed unit, sec. 15, T33N, R6E, Idaho Co., Idaho.
34. Juntura (?) Fm., Otis Creek, sec. 32, T19S, R36E, Harney Co., Oregon.
35. Lake Britton, unnamed unit, sec. 29, T37N, R3E, Shasta Co. California.
36. Latah (?) Fm., Hangman Valley, sec. 6, T24N, R43E, Spokane Co., Washington.
37. Raft River Fm., Burley, sec. 35, T10S, R27E, Cassia Co., Idaho.
38. Lower (?) part of the Columbia River Basalt Group, Seven Mile Creek, sec. 19, T2S, R33E, Umatilla Co., Oregon.
39. Amoco Lynn Reese No.1 well, sec. 17, T12N, R1E, Cache Co., Utah.
40. Amoco Milford Federal No.1 well, sec. 19, T15N, R27E, Lemhi Co., Idaho.
41. Truckee Fm. (middle member), Fernley, sec. 8, T19N, R26E, Churchill Co., Nevada.
42. New Pass, unnamed unit, unsurveyed T19N, R40E, Lander Co., Nevada.
43. Oviatt Creek, unnamed unit, sec. 12, T39N, R1E, Clearwater Co., Idaho.
44. Poison Creek Fm., Reynolds Creek, sec. 2, T2S, R3W, Owyhee Co., Idaho.
45. Poison Creek Fm., sec. 17, T11N, R6W, Washington Co., Idaho.
46. Ringold Fm., White Cliffs, Columbia River, sec. 1, T10N, R28E, Franklin Co., Washington.
47. Big Smokey Valley, unnamed unit, unsurveyed T2N, R38E, Esmeralda Co., Nevada.
48. Southern Stillwater Mountains, unnamed unit, sec. 22, T18N, R31E, Churchill Co., Nevada.
49. Squaw Creek Member, Ellensburg Fm., sec. 9, T14N, R19E, Yakima Co., Washington.
50. Sucker Creek Fm., Leslie Gulch, sec. 28, T24S, R46E, Malheur Co., Oregon.
51. Swayze Creek, unnamed unit, sec. 6, T12S, R44E, Baker Co., Oregon.
52. Thousand Creek Fm., unsurveyed T46N, R25E, Humboldt Co., Nevada.
53. Beaverdam Fm., Trapper Creek, sec. 2, T15S, R20E, Cassia Co., Idaho.
54. Truckee Fm. (middle member), Bradys Hot Spring, sec. 21, T23N, R27E, Churchill Co., Nevada.
55. Truckee Fm. (middle member), Browns Hill, sec. 33, T23N, R27E, Churchill Co., Nevada.

56. Truckee Fm. (lower member), Hot Springs Mountains, sec. 36, T22N, R27E, Churchill Co., Nevada.

57. Truckee Fm. (middle member), Nightingale, sec. 18, T24N, R26E, Churchill Co., Nevada.

58. Tulare Fm., La Ceja Ridge, Kettleman Hills, secs. 26/35, T21S, R17E, Kings Co., California.

59. Ellensburg Fm., Vantage, sec. 17, T18N, R23E, Grant Co., Washington.

60. "Yonna" Fm., Dorris, sec. 11, T47N, R1E, Siskiyou Co., California.

61. "Yonna" Fm., Klamath Falls, sec. 23, T38S, R8E, Klamath Co., Oregon.

62. "Yonna" Fm., Yonna Valley, sec. 23, T38S, R11.5E, Klamath Co., Oregon.

63. U.S.G.S. Diatom Localities 1019, 1020, unnamed unit, Drewsey, sec. 14, T20S, R36E, Harney Co., Oregon.

64. U.S.G.S. Diatom Locality 1022, Bully Creek Fm., Westfall, Harper Basin, sec. 15, T18S, R41E, Malheur Co., Oregon.

65. U.S.G.S. Diatom Locality 1023, Bully Creek Fm., Harper Basin, sec. 34, T19S, R42E, Malheur Co., Oregon.

66. U.S.G.S. Diatom Locality 1024, Bully Creek Fm., Harper Basin, sec. 34, T18S, R41E, Malheur Co., Oregon.

67. U.S.G.S. Diatom Locality 1030, Swayze Creek, lake beds of Burnt River, sec. 11, T11S, R43E, Baker Co., Oregon.

68. U.S.G.S. Diatom Locality 1187, "Truckee" lake beds, 10 miles N of Virginia City, Virginia Range, Storey Co., Nevada.

69. U.S.G.S. Diatom Locality 1690, Forty-nine Camp, Washoe Co., Nevada, upper part of the Cedarville Fm., 17 miles E of N of Cedarville, California.

70. U.S.G.S. Diatom Locality 2280, unnamed unit, 15 miles NE of Weiser, Washington Co., Idaho.

71. U.S.G.S. Diatom Locality 2281, unnamed unit, 2.5 miles NE of Whitebird, Idaho Co., Idaho.

72. U.S.G.S. Diatom Locality 2289, unnamed unit, about 2.5 miles NE of Arrow Junction, Nez Perce Co., Idaho.

73. U.S.G.S. Diatom Locality 3707, unnamed unit, Goose Creek, sec. 35, T14S, R20E, Cassia Co., Idaho.

74. U.S.G.S. Diatom Locality 3394, Esmeralda Fm., Cedar Mountain, T8N, R38E, Nye Co., Nevada.

75. U.S.G.S. Diatom Locality 4213, Silvies Valley, unnamed unit, sec. 36, T17S, R31E, Grant Co., Oregon.

76. U.S.G.S. Diatom Locality 5678, Latah Fm., Shelly Lake, sec. 24, T25N, R44E, Spokane Co., Washington.

77. U.S.G.S. Diatom Locality 5679, Latah Fm., sec. 15, T24N, R43E, Spokane Co., Washington.

78. U.S.G.S. Diatom Locality 5681, Latah (?) Fm., Peone, sec. 27, T26N, R44E, Spokane Co., Washington.

79. U.S.G.S. Diatom Locality 6007, unnamed unit, sec. 20, T24N, R26E, Churchill Co., Nevada.

80. U.S.G.S. Diatom Locality 6035, unnamed unit, N. Santiam River, T11S, R7E, Linn Co., Oregon.

81. U.S.G.S. Diatom Locality 6364, 6371, 6373, unnamed unit, Durkee, sec. 23, T11S, R43E, Baker Co., Oregon.

82. U.S.G.S. Diatom Locality 6368, unnamed unit, Durkee, sec. 20, T11S, R43E, Baker Co., Oregon.

83. Aldrich Station Formation, type section, 38°29'30'' N, 118°53'21'' W, Mineral Co., Nevada.

84. Kate Peak Formation, Eagle-Picher Diatomite Quarry, Clark Siding, Nevada, T20N, R23E, Storey Co., Nevada.

85. Mascall Fm., Aldrich Mtn., Meadow locality, Grant Co., Oregon (UCMP loc.P4123); SE1/4 sec. 14, T13S, R28E; N. side of east fork of John Day River.

86. Juntura Fm.(?), Harney Co., Oregon, Stinking Water flora (UCMP loc. P4121); NW1/4 sec. 17, T21S, R35E.

87. Mascall Fm., White Hills, Belshaw ranch locality, Grant Co., Oregon (UCMP loc. P3735); N. center sec. 13, T13S, R28E.

88. Mascall Fm., Blue Mtns., Vinegar Creek, Grant Co., Oregon (UCMP loc. P5404); sec. 17, T10S, R35E; 1 mile NW of Bates on road to Susanville.

89. Unnamed unit, Thorn Creek, Boise Co., Idaho (UCMP loc. P4600); sec. 28, T5N, R5E.

90. Hole-in-the-Wall Diatomite, Gooding Co., Idaho along the drainage of Clover Creek; NW1/4 sec. 12, T4S, R13E.

91. Hole-in-the-Wall Diatomite, Gooding Co., Idaho; NE1/4 sec. 19, T3S, R13E.

92. Quiburis Fm., Edgar Canyon, San Pedro Valley, Arizona, 900 ME, 200m N of SW corner, Pima Co.; sec. 21, T11S, R18E.

93. Esmeralda Fm., Black Spring, Nye Co., Nevada; sec. 19, T8N, R38E.

94. N.Fork Fitsum Creek, Valley Co., Idaho; sec. 6, T19N, R6E.

95. Esmeralda Fm., Cedar Spring, Nye Co., Nevada; unsurv.T8N, R38E.

96. U.S.G.S. Diatom Locality 642, Baker Co., Oregon; sec. 8, T8S, R42E.

97. U.S.G.S. Diatom Locality 1013, Clover Creek District, Baker Co., Oregon; sec. 11, T8S, R42E.

98. U.S.G.S. Diatom Locality 1031, Malheur Co., Oregon; sec. 2, T15S, R42E.

99. U.S.G.S. Diatom Locality 1037, Grant Co., Washington; T28N, R30E, (Grand Coulee Flora).

100. U.S.G.S. Diatom Locality 1133, 4 miles E.of Basalt, Esmeralda Co., Nevada; T2N, R34E.

101. U.S.G.S. Diatom Locality 1186, "Truckee" lake beds, Chalk Bluff, 3 miles W. of Reno, Washoe Co., Nevada; T19N, R19E.

102. U.S.G.S. Diatom Locality 2268, Wikiup Damsite, Deschutes River, Deschutes Co., Oregon; T22S, R9E.

103. U.S.G.S. Diatom Locality 3544, Thousand Creek Beds, Humboldt Co., Nevada; unsurv. T45N, R26E.

104. U.S.G.S. Diatom Locality 4671, Santa Fe Fm., Rio Arriba Co., New Mexico; T21N, R7E.

105. U.S.G.S. Diatom Locality 4690, Alturas Fm., Modoc Co., California; sec. 7, T42N, R12E.

106. U.S.G.S. Diatom Locality 5682, Latah Fm., Mead, Spokane Co., Washington; sec. 14, T26N, R43E.

107. U.S.G.S. Diatom Locality 5935, Teewinot Fm., Teton Co., Wyoming; sec. 36, T42N, R116W.

108. IW-7, Poison Creek Fm., Washington Co., Idaho; SW SW sec. 29, T12N, R6W.

109. IW-8, Poison Creek Fm., Washington Co., Idaho; SW SW sec. 32, T12N, R6W.

110. IW-9, Poison Creek Fm., Washington Co., Idaho; SE SE sec. 19, T12N, R6W.

111. IW-13, Idaho Group, Washington Co., Idaho; NE NE sec. 19, T12N, R4W.

112. Amoco Becharof No.1 well, 57. 78°N, 157. 11°W, Alaska Peninsula, Alaska.

113. U.S.G.S. Diatom Locality 4070, Furnace Creek Fm., Inyo Co., California; 1.15 miles N77°W of Travertine Point, road cut on south side of Highway 190. Hard gray limestone 3 ft. below base of travertine.

114. Coal Valley Fm. *sensu* Axelrod, 1958, Washoe Co., Nevada; roadcut along Highway 40 W of Reno, sec. 18, T19N, R19E.

115. Coal Valley Fm. *sensu* Axelrod, 1958, Washoe Co., Nevada; Verdi flora locality, sec. 16, T19N, R18E.

Appendix 2. Paleogene Diatom Sample Localities

1. Dewey beds, Dewey Mine, Thunder Mountain district, Valley Co., Idaho (Leo ard and Marvin 1982).

2. Horsefly Eocene beds, Horsefly Mine section, Horsefly, British Columbia, Can ada (Wilson 1980).

3. Climbing Arrow Fm., NW SW sec. 3, T8S, R5W, Ruby Basin, Madison Co., Montana.

4. Passamari Fm., N1/2 SW1/4 sec. 13, T9S, R5W, Caldwell Springs, Ruby Basin, Madison Co., Montana.

5. Passamari Fm., NE SE1/4 sec. 21, T8S, R5W, Sweetwater Creek, Ruby Basin, Madison Co., Montana.

6. Passamari Fm., center W1/2 sec. 13, T8S, R5W, Ruby Basin, Madison Co., Montana.

7. Cabbage Patch Fm., SE1/4 SE1/4 sec. 1, T10N, R12E, or center W1/4 SW1/4, sec. 6 T10N, R11W, Deer Lodge Basin, Granite or Powell Co., Montana.

8. Cabbage Patch Fm., center E1/4 NW1/4 SW1/4 sec. 30, T9N, R10W, Deer Lodge Basin, Powell Co., Montana.
9. Cabbage Patch Fm., S1/2 N1/2 SW1/4 sec. 12, T10N, R12W, Deer Lodge Basin, Granite Co., Montana.
10. Cabbage Patch Fm., SW SW sec. 11, T10N, R12W, Deer Lodge Basin, Granite Co., Montana.
11. Renova? Fm., SE sec. 3, T11N, R12W, Douglass Creek Basin, Powell Co., Montana (Konizeski 1961).
12. Blacktail Deer Creek Fm., SE1/4 NE1/4 SW1/4 sec. 8, T11S, R6W, Beaverhead Co., Montana.
13. "Cook Ranch" volcanics, NE1/4 sec. 7, T11S, R8W, Beaverhead Co., Montana.
14. Currant Tuff, Spidle Ranch, sec. 12, T12N, R60E, White Pine Co., Nevada (Firby 1973).
15. Illipah Fm., Indian Springs mammal locality, 40 miles west of Ely, NE SE sec. 10, T18N, R59E, White Pine Co., Nevada.
16. Florissant lake beds, MacGinnite (1953) loc. no. 3, Colorado.

Holocene Diatoms From a Mexican Crater Lake — La Piscina de Yuriria

by

S. Metcalfe

School of Geography and Earth Resources, University of Hull,
Hull HU6 7RX, England

and

P. Hales

Tropical Palaeoenvironments Research Group, School of Geography,
Mansfield Road, Oxford OX1 3TB, England

with 5 figures, 1 table, and 1 plate

Abstract: La Piscina de Yuriria is a small explosion crater in southern Guanajuato, Mexico (20° 13'N, 101° 08'W). In 1981, the crater contained a shallow (2 m), alkaline (pH 9.75) lake; by 1989 the basin was completely dry.

A 4 m core was recovered from the basin in 1981. The sediments consisted of gyttja, dark reddish-brown to dark grey in color. Water samples and modern diatoms were collected in 1982, when the water had a pH of 11, electrical conductivity of 26,000 µS cm^{-1} and a composition dominated by Na-CO_3-Cl.

The core has been analyzed with respect to its diatom flora, major elements and loss-on-ignition, magnetic susceptibility and, $\delta^{13}C$. Radiocarbon dates have been obtained from eight levels, the oldest being 4100 +/- 200 yr BP at 375–380 cm. The diatom assemblages in much of the core are dominated by *Navicula halophila* (Grunow) Cleve and/or *N. elkab* O. Müller. The separation of these two species remains uncertain. The spores of *Chaetoceros muelleri* Lemmermann are present and abundant in parts of the core.

The *N. halophila*/*N. elkab* assemblages are similar to those found in lake margin samples in 1982 and probably reflect shallow, warm, saline conditions of high conductivity and alkalinity. Periods when *C. muelleri* is abundant may indicate an increasing importance of Cl relative to CO_3.

Diatom preservation is poor in parts of the core and differential preservation must be considered. The core assemblages do, however, appear to record a series of minor climatic oscillations. The timing of these oscillations and of episodes of accelerated erosion is comparable with other sites in the region.

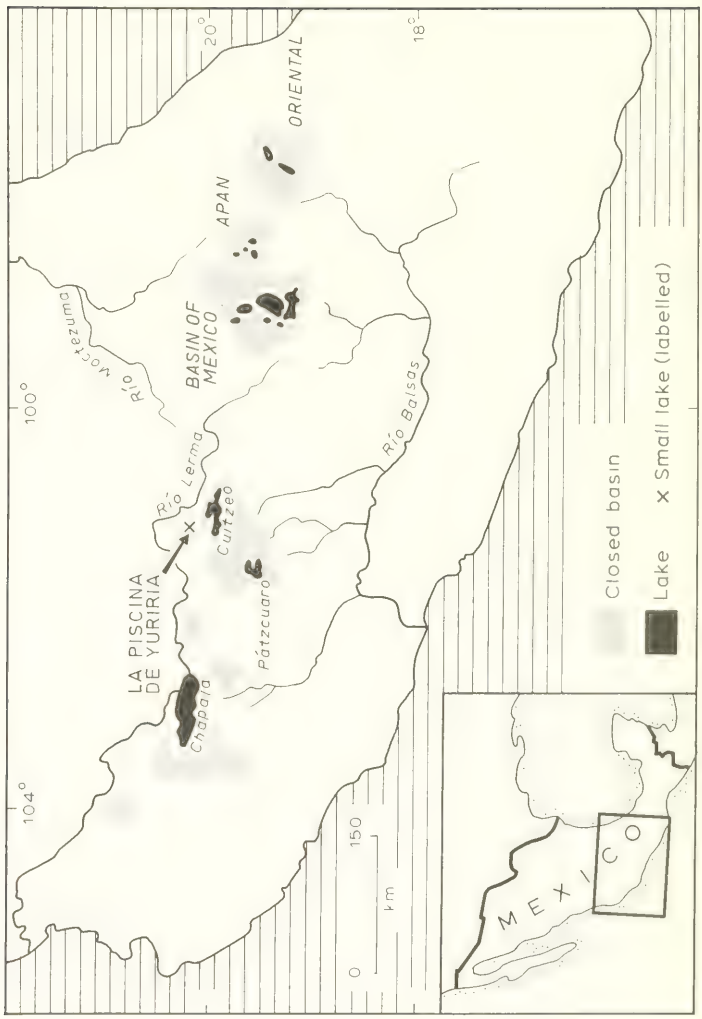


FIGURE 1. Location map La Piscina de Yuriria, Guanajuato.

Introduction

La Piscina de Yuriria was a small, topographically closed lake in a steep-sided, explosion crater in the south of the state of Guanajuato (20° 13'N, 101° 08'W) (Fig. 1). The climate of the area is subhumid with 700–800 mm of precipitation per annum (Secretaría de Programacion y Presupuesto 1980). In 1981, the lake was 2 m deep, saline, and alkaline (pH 9.75); by 1982 the depth was reduced to 1.5 m and by 1989 the basin was completely dry, with a white salt crust across the floor of the crater.

La Piscina de Yuriria was visited in 1981 when preliminary water and algal sampling was carried out. In 1982, a more comprehensive collection was made. Water and algal samples were taken from a number of sites around the lake and from springs found at the foot of the crater's inner wall. The water in the center of the lake had a pH of 11, electrical conductivity (EC) of 26,000 $\mu S\ cm^{-1}$, and was of Na-CO_3-Cl type. The level of total dissolved solids put the water into the very saline category of the U. S. G. S. classification. Although a large number of spring sites were found, most of these were dry in 1982. Where water was present, it was considerably fresher than that in the lake, with pH 7.5, EC 500 $\mu S\ cm^{-1}$, and of Na-HCO_3 type.

Details of the modern diatom flora have been given elsewhere (Metcalfe 1985). Sediment from the water/mud interface yielded a diatom assemblage in which *Navicula elkab* O. Müller (22 %) and *N. halophila* (Grunow) Cleve (13 %) were most abundant, with a wide variety of *Nitzschia* spp. (e.g., *N. gandersheimiensis* Krasske, *N. frustulum* (Kützing) Grunow, *N. communis* Rabenhorst, *N. palea* (Kützing) W.Smith). Lake margin water samples had a similar flora. A coiled filamentous cyanobacterium (blue-green alga), possibly *Lyngbya contorta* Lemm. was abundant in some lake margin samples; *Rivularia* or *Gleotrichia* were also present.

Metcalfe (1988) discusses the possible relationship between lake water chemistry and diatom assemblages in the context of Central Mexico. La Piscina de Yuriria is clearly a highly evolved lake in the context of the model outlined by Eugster and Hardie (1978). This model shows the major geochemical pathways followed as evaporation proceeds within a closed basin lake. Plotting anion and cation composition from a range of sites in the volcanic setting of Central Mexico illustrates that cation composition shows a gradient from high Ca^{2+} lakes to those high in Na^+ and K^+, while anions display a broad trend from CO_32-/HCO_3- to Cl^- domination. This change in composition generally corresponds to reduced precipitation and/or increased evaporation. These changes are as described in pathway IIIA of the Eugster and Hardie model. La Piscina de Yuriria lies clearly towards the end of this chemical and climatic gradient, with $Na^+ > K^+$ and relatively high Cl^-. The apparent sensitivity of diatoms to changes in the dominant cations and anions may be used to identify changing degrees of evaporative concentration, presumably in response to climatic change.

Ecological data for Mexican diatoms are still quite scarce (Metcalfe 1988; Bradbury 1989). However, many volcanic lakes of East Africa are of similar chemical composition (Na-HCO_3/CO_3-Cl) and a considerable amount of information is available concerning the diatoms in these lakes (e.g., Hecky and Kilham 1973; Richardson et al. 1978; Gasse et al. 1983). Although some caution is needed in applying ecological data from one area to diatoms from another, this information has been used extensively in the present study.

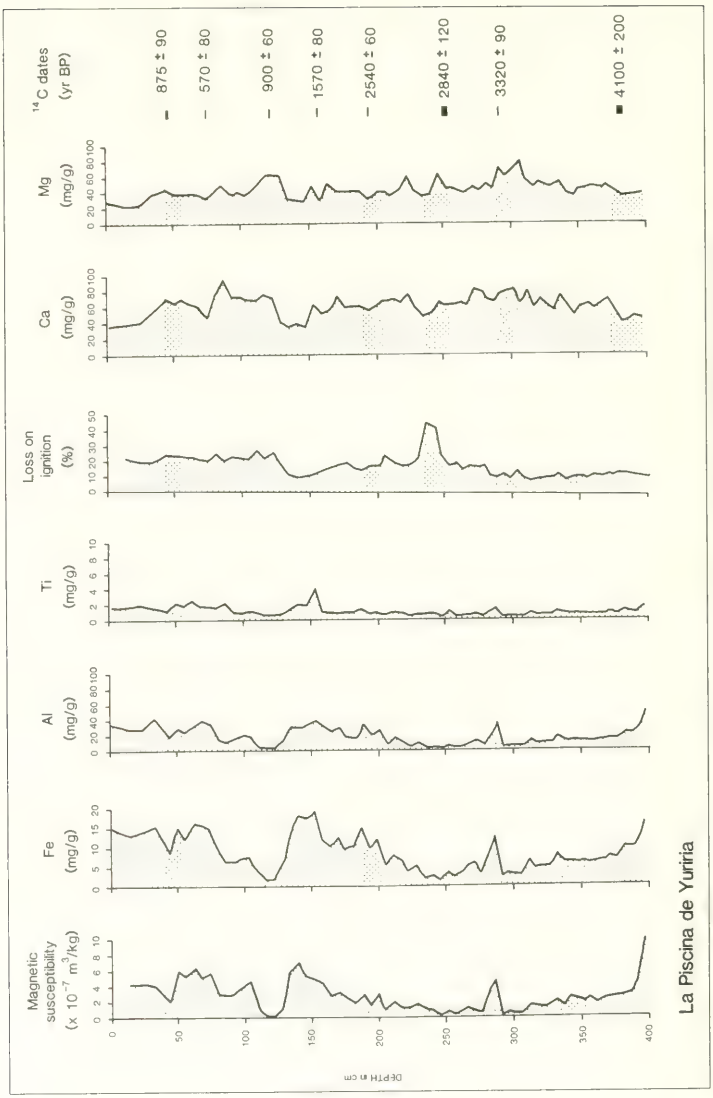


FIGURE 2. Magnetic susceptibility (χ), loss-on-ignition, and major elements from the La Piscina de Yuriria core.

Results and Discussion

Sediments

In 1981 a 4 m core was recovered from the center of La Piscina de Yuriria, using a modified Livingstone corer. The sediments consisted of gyttja, dark reddish-brown to dark grey in color. Radiocarbon dates have been obtained from eight levels in the core (Table 1). All the dates have been carried out by AMS (accelerator mass spectrometry) and have been provided by Simon Fraser University and by the Oxford Radiocarbon Accelerator Unit. Core depths have been adjusted to allow for apparent compaction of the sediment during collection. It should be noted that the Oxford dates have not yet been corrected for isotopic fractionation, although the necessary $\delta^{13}C$ measurements are in progress. Correction will probably make these dates a little older.

The core has been analyzed for major elements, loss-on-ignition, magnetic susceptibility (χ), carbonate content, $\delta^{13}C$ and $\delta^{18}O$ (by PEH) (Figs. 2, 3). The core sediments appear to provide a good record of disturbance episodes within the catchment (based on χ, Fe, Al, and Ti in particular). Four such episodes have been identified: In the lowest 10 cm of the core (just below the date of 4100 +/- 200 yr BP); between 290 and 270 cm (bracketed by radiocarbon dates of 3320 +/-90 and 2840 +/- 120 yr BP); between 180 and 130 cm (bracketed by dates of 2450 +/- 60 and 900 +/- 600 yr BP); and above 80 cm (< 900 yr BP) (Metcalfe et al 1989). Whether these episodes reflect climatic change or human impact (or both) is not clear from the bulk sediment chemistry alone. Pollen analysis of the core is in progress (R. A. Perrott), which may help to resolve this question.

The chemistry of the lake sediments will be described in detail elsewhere, but will be referred to when appropriate.

Diatoms

Diatom samples were prepared at 10 cm intervals using standard methods (Battarbee 1986) and identifications were made with reference to several floras (e.g., Hustedt 1930–66; Patrick and Reimer 1966, 1975; Schoeman and Archibald 1977; Krammer and Lange Bertalot 1988). Where possible at least 400 valves were counted at each level, and the results are given as percentages (Fig. 4). The changing abundances of the major genera present are given in Figure 5.

The major taxonomic problem encountered was the separation of *Navicula elkab* from *N. halophila*, itself a highly variable taxon especially if the approach of Krammer and Lange-Bertalot (1986) is followed. The problems of identification in the absence of type material, and the need for a revised definition of *N. elkab* have been discussed previously in detail (Metcalfe 1990). The correct identification of this species is important as it does appear to have a distinct ecology, being typical of hyperalkaline Na-CO_3 lakes where Cl^- is an important anion (Hecky and Kilham 1973; Richardson et al. 1978; Gasse 1986). Valves identified as *N. elkab* from La Piscina de Yuriria range in length from 16–34 µm and are about 5 µm wide. The striae vary from parallel to slightly radiate and are usually 22 in 10 µm in the central portion, fewer than indicated by Muller in his original description (Müller 1899). Some of the valves are illustrated in Figures 6–9.

At one level in the core (122 cm), the assemblage was dominated by a small *Navicula* species. This has been identified as *N. muralis* Grunow (Hustedt 1961–1966) although the valve shape was sometimes more like that illustrated for *N. pseudomuralis* Hustedt. Hustedt's version of *N. muralis* has not been included in the revision proposed by Krammer and Lange-Bertalot (1986).

The cysts of *Chaetoceros muelleri* Lemmermann were quite abundant in the core and a few individuals were present in lake margin and modern surface sediment samples. Al-

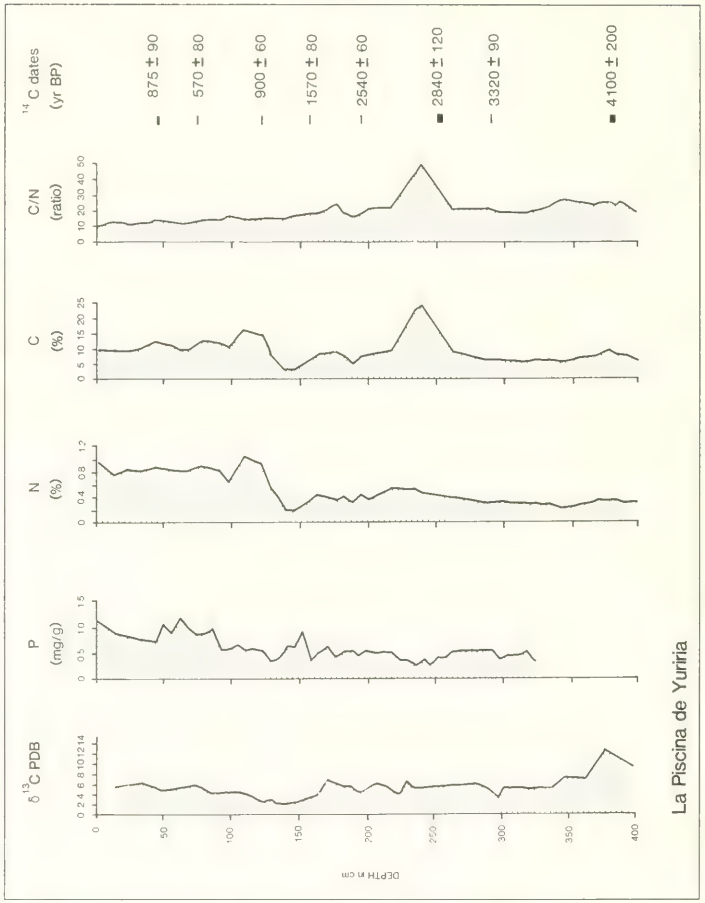


FIGURE 3. ^{13}C and selected elements from the La Piscina de Yuriria core.

though the genus is essentially marine, this taxon has been reported from Cl^- rich "fresh" waters (Gasse 1986; Bradbury 1989). Fritz and Battarbee (1988) also record abundant *Chaetoceros*, usually as cysts, in saline (EC > 3000 µS cm^{-1}) lakes in the northern Great Plains, although the chemistry of the brines is not specified. These authors also point out that *Chaetoceros* cysts, and other robust and heavily silicified diatoms, may be over-represented in the sediments of shallow, saline lakes due to their resistance to both dissolution and breakage. In La Piscina de Yuriria, the diatom assemblages from the top part of the core (see Zone VIII below) were similar to those in the surface sediment sample collected in 1982, although the numbers of *C. muelleri* cysts were much higher in the former than in the latter. It seems likely, therefore, that this taxon may be over-represented in older sediments.

Based on a visual assessment of changing assemblages, eight diatom zones have been identified in the core from La Piscina de Yuriria. These are shown on Figure 5 and will form the basis for discussion.

Zone I (samples 396–97 to 336–37 cm) is dominated by *N. elkab* and *N. halophila*, with *Nitzschia frustulum*, *N. palea*, and *Rhopalodia gibberula* (Ehrenberg) O. Müller. *Nitzschia frustulum* is generally more abundant where *N. elkab* is greater than *N. halophila*. Both *N. halophila* and *N. elkab* are generally periphytic, but may be found in the plankton in shallow, turbulent lakes (Hecky and Kilham 1973; Gasse 1986). They are found in water of high pH and conductivity and, according to Gasse (1986), *N. elkab* is common in highly alkaline waters (26.8 meq l^{-1}). *Nitzschia frustulum* is also indicative of high alkalinities (80 meq l^{-1} according to Hecky and Kilham 1973) and an obligate N-heterotroph (Cholnoky 1968), as is *N. palea*. It would seem, therefore, that Zone I reflects a shallow, highly alkaline eutrophic lake, possibly one in which blue-green algae formed an important part of the algal population (Hecky and Kilham 1973). The radiocarbon date of 4100 +/- 200 yr BP lies just above the *N. elkab/Nitzschia* spp. peak. Based on the sediment chemistry (Fig. 2) the bottom of this core records a period of detrital sediment input. Diatom preservation was generally quite poor in this zone although valves of *R. gibberula*, *Anomoeoneis costata* (Kützing) Hustedt, and *Denticula elegans* Kützing were heavily silicified and relatively well preserved, a consistent feature throughout the core. The implications of this for differential preservation and subsequent palaeoecological interpretation must be borne in mind.

The base of Zone II (326–27 to 296–97 cm) is marked by a sharp increase in *A. costata* and *A. sphaerophora* (Ehrenberg) Pfitzer, *R. gibberula*, *C. muelleri*, *D. elegans*, and *D. elegans* f. *valida* Pedicino, with a corresponding decline in *N. halophila* (in particular) and *N. elkab*. *Anomoeoneis sphaerophora* and *A. costata* are both alkaline water forms (50 meq l^{-1}), usually benthic but occurring in the plankton of shallow, alkaline lakes (Gasse 1986). The increasing abundance of *C. muelleri*, and the presence of diatoms such as *Amphora coffeaeformis* (Agardh) Kützing, probably reflects increasing Cl^- and salinity levels. Cl^- may have replaced CO_3^{2-} as the dominant anion. An assemblage very similar to that in Zone II was identified by Gasse (1987) as representative of mesosaline, very shallow ponds with Cl^- (and SO_4^{2-}) rich water. The assemblage in this zone is also similar to Bradbury's (1989) saline marsh group. Core chemistry would appear to indicate stability in the catchment, which may simply be a product of the lack of runoff. A radiocarbon date of 3320 +/- 90 yr BP was obtained from 291–292 cm, just between this zone and the overlying Zone III.

Three samples are included in Zone III (286–287 to 266–267 cm), which are marked by a return to a *N. halophila/N. elkab* flora, few if any *Chaetoceros* spores, and much lower numbers of *Anomoeoneis*. *Rhopalodia gibberula* and *Nitzschia frustulum* persist. Valve

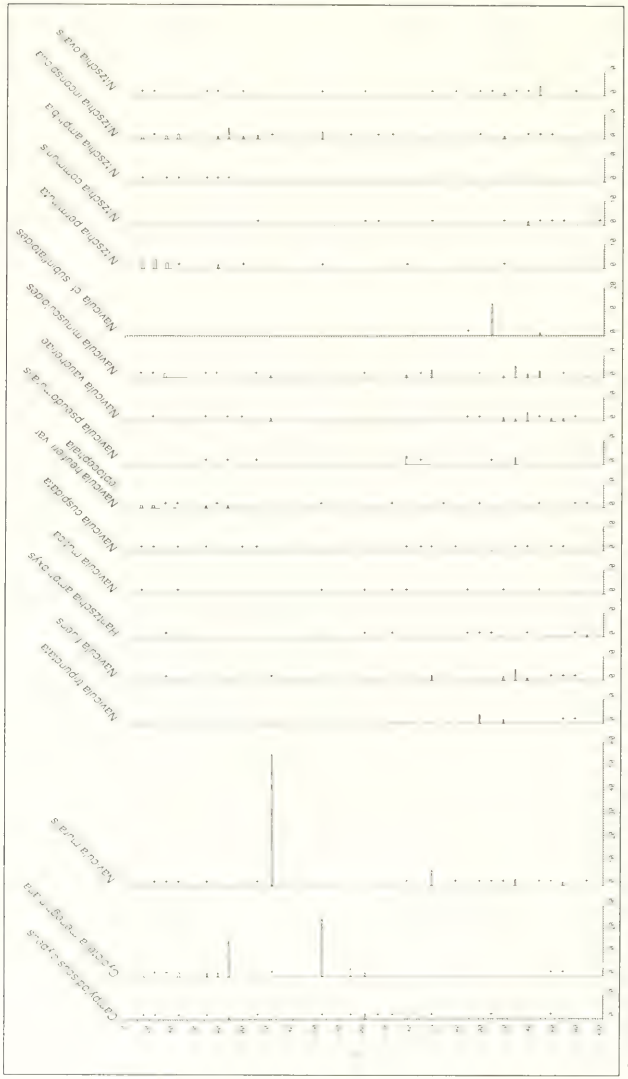


FIGURE 4. Diatom diagram La Piscina de Yuriria.

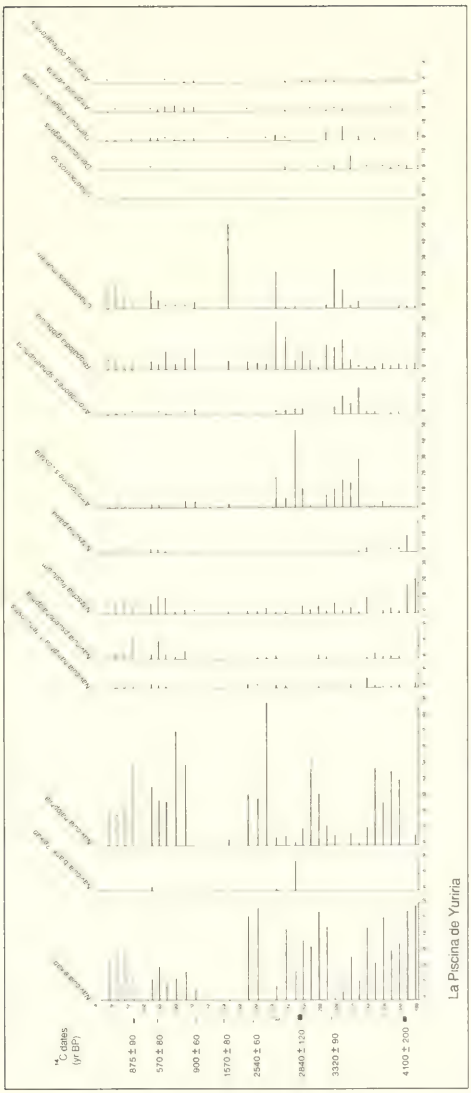


FIGURE 4, continued. Diatom diagram La Piscina de Yuriria.

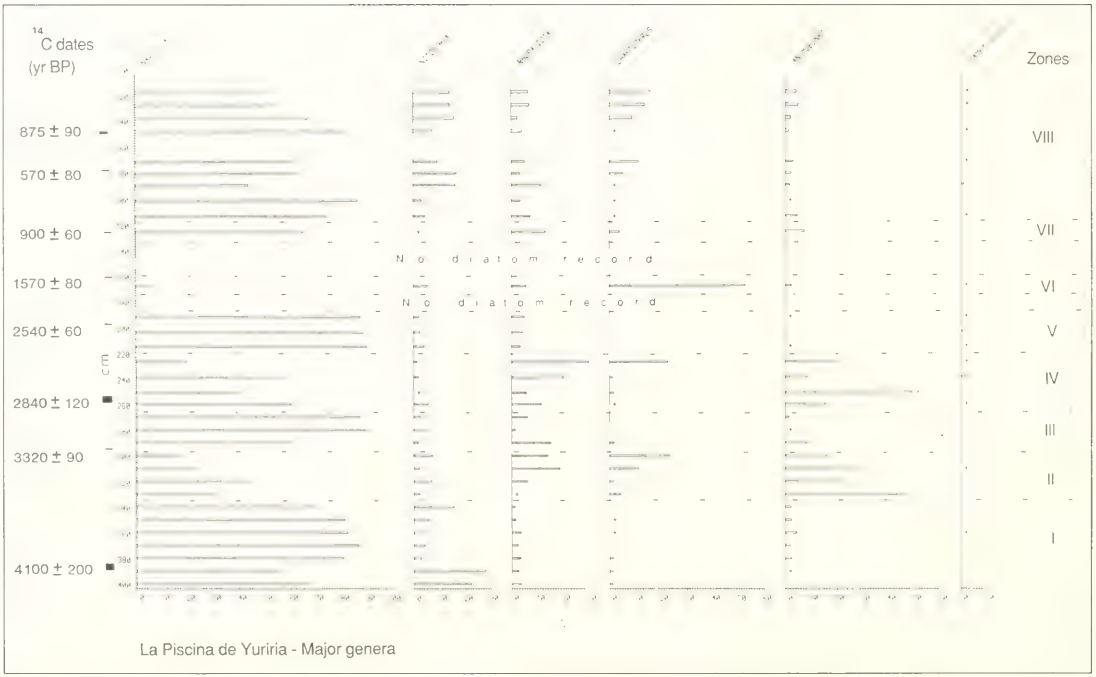


FIGURE 5. Major diatom genera in the La Piscina de Yuriria core.

TABLE 1. Radiocarbon dates (by AMS) from La Piscina de Yuriria.

Depth cm	Laboratory number	Date ^{14}C yr BP
44–46	0xA-1963	875 ± 90
74–75	0xA-1964	570 ± 80
122–123	0xA-1965	900 ± 60
157–158	0xA-1966	1570 ± 80
194–195	0xA-1967	2540 ± 60
250–255	RIDDL-62	2840 ± 120

preservation is generally better than in Zones I and II. Although still alkaline, it seems that the lake water was more dilute and that it reverted to being Na-CO_3 dominated. This assemblage shows some similarities to that recorded by Gasse (1987) for mesosaline Na-CO_3-rich open water. The sediment chemistry shows clear signs of disturbance in the lower part of this zone with peaks in χ, Fe, and Al (see Fig. 2). It is possible that increased precipitation resulted in a relative freshening of the lake but led to greater erosion within the catchment. This episode of increased runoff is bracketed by dates of 3320 +/- 90 yr BP from 291–292 cm and 2840 +/- 120 yr BP from 250–255 cm.

The period of moister conditions was obviously short-lived as Zone IV (256–57 to 223 cm) has a flora and trend similar to that in Zone II. *Navicula elkab* remains important, but *A. costata*, *R. gibberula*, and *C. muelleri* become successively more abundant going up through the zone. Small *Navicula* species indicative of elevated pH (8), such as *N. muralis* and *N. minusculoides* Hustedt (Cholnoky 1968) are also present. Following the pattern in Zone II, the increasing percentage of *C. muelleri* spores (23 % at 223 cm) is taken to indicate the evolution of the lake from a Na-CO_3 towards a Na-Cl composition. Differential preservation may again be significant. The sediment analyses show a decrease in disturbance indicators (χ, Fe, Al, Ti) over this interval (Fig. 2).

The pattern shown at the Zone II/III boundary is repeated between Zones IV and V, although the almost total disappearance of *Chaetoceros* and *Anomoeoneis* and the dominance of *N. halophila* (89 % at 211 cm) suggests an even more abrupt change in conditions. In the upper part of the zone *N. elkab* becomes more abundant. Valve preservation is generally poor and becomes worse, being particularly poor in the sample from 188 cm. A ^{14}C date of 2540 +/- 60 was obtained from a sample at 194–195 cm.

The overlying 60 cm of the core (ca. 185–125 cm) has only a patchy diatom record. No count was possible from 176 cm. A single sample from 164 cm forms Zone VI, and then there is another break in the record. In the Zone VI sample *C. muelleri* and *Cyclotella meneghiniana* Kützing are predominant (53 % and 24 %, respectively). Otherwise only *R. gibberula* exceeds 5 % of the count. *Chaetoceros muelleri* excepted, valve preservation was very poor with many fragments and abundant mineral debris. Whether the species recorded in the count from this level in any way represent a life assemblage is questionable. Indicators of disturbance in the catchment increase over this period, although there are no signs in the diatom record that this could be attributed to increased runoff. Whether the lake actually dried out at any time between the top of Zone V and the bottom of Zone VII (122 cm) is not clear, although it is likely that it was ephemeral. Preliminary pollen analysis shows a peak of *Juniperus* at 140 cm, which would tend to suggest dry conditions (R.A. Perrott, pers. comm.). A radiocarbon date of 1570 +/- 80 yr BP was obtained from 157–158 cm and a date of 900 +/- 60 yr BP from 122–123 cm, just below where the diatom record resumes.

The top 122 cm of the core contains a diatom record that has been divided into two zones (VII and VIII). Zone VII consists of a single sample, dominated by *Navicula muralis* (55 %). According to Hustedt (1961–1966), *N. muralis* is often found in algal mud flats or amongst aquatic plants. High total organic carbon (TOC) (Fig. 3) may also reflect this. A very shallow, alkaline but low-energy environment may be envisaged within a stabilized catchment (low detrital indicators [Fig. 2]). Good valve preservation in this sample supports this idea.

Zone VIII includes the samples from 110 to 14–16 cm and has two radiocarbon dates: 570 +/- 80 yr BP from 74–75 cm and 875 +/- 90 cm from 44–46 cm. The assemblages in this zone consist mainly of *N. halophila* (and *N. pseudohalophila* Cholnoky) and *N. elkab.* *Nitzschia* species increase in abundance, mainly above 86 cm, and include *N. frustulum*, *N. palea*, *N. inconspicua* Grunow, and *N. perminuta* (Grunow) M. Peragallo. *Rhopalodia gibberula* is quite abundant throughout and *C. muelleri* increases in abundance up the core to 15 % in the top sample. Many of the *Nitzschia* species recorded here are described by Cholnoky (1968) as obligate N-heterotrophs. The core chemistry shows high levels of organic C, N, and total P in this zone (Fig. 3) and may well reflect cultural eutrophication of the lake. Severe catchment disturbance over this period is indicated by generally higher χ, Fe, Al, and Ti (Fig. 2). This disturbance might explain the apparently anomalous ^{14}C date from 44–46 cm (875 +/- 90 yr BP), if old carbon was washed in to the lake. Using Stuiver and Pearson's calibration program (1986), the radiocarbon date of 570 +/- 80 yr BP from 74 cm equates to AD 1398, so the top part of the core covers the later Postclassic (AD 900–1520) and Hispanic periods. The town of Yuriria on the north flank of the crater is known to have been a garrison town and important local ceremonial center over this period (Gomez de Orozco 1972). The diatoms in the upper part of Zone VIII may reflect increasing evaporative concentration of the lake and an increase in Cl^- in the water. However, valve preservation was particularly poor in the top two samples, and their exact significance is uncertain. The recent desiccation of the basin is probably due more to the effects of regional groundwater pumping for extensive irrigation projects (Secretaría de Programacion y Presupuesto 1980) than to changes in precipitation.

Conclusions

The diatom record from La Piscina de Yuriria displays a sequence of diatom assemblages that may be explained in terms of changes in the abundance of Cl^- relative to $CO_3 2-$ following the Eugster and Hardie model of evaporative concentration. The lake sampled in 1982 had $CO_3 > Cl$ and a flora similar to that in core Zones I, III, V, and VIII. Sections of the core with assemblages of *C. muelleri*, *R. gibberula*, and *Anomoeoneis* spp. (Zones II, IV, and VI) are believed to indicate periods when Cl^- was the dominant anion, presumably due to less precipitation and/or greater evapotranspiration. The driest period recorded appears to be between 1570 +/- 80 yr BP and 900 +/- 60 yr BP. This interval was also dry at other sites in Central Mexico and corresponds to the cultural "collapse" of the Epiclassic or late Classic periods. However, caution is needed in interpreting records from well-mixed, shallow, saline, and highly alkaline lakes due to problems of differential preservation. In this core, cysts of *C. muelleri* may be overrepresented.

There are similarities between the disturbance record in this catchment and those from elsewhere in the region (Metcalfe et al. 1989). The most recent episode covers the late Postclassic and Hispanic periods, which is in keeping with other sites within, or on the margins of, the Tarascan state.

Acknowledgements

This research was funded primarily by NERC studentships for PEH and SEM. The core was taken by Alayne Street-Perrott, Alan Perrott, and SEM. The authors would like to thank Alayne Street-Perrott for her advice and encouragement. We also thank John Garner for his photographic work and the Faculty Board of Anthropology and Geography and the School of Geography, Oxford, for grants towards the fieldwork.

Literature Cited

BATTARBEE, R. W. 1986. Diatom Analysis. Pp. 527–570 *in* Handbook of Holocene Palaoecology and Palaeohydrology, B. E. Berglund ed., Wiley, Chichester.

BRADBURY, J. P. 1989. Late Quaternary lacustrine palaeoenvironments in the Cuenca de Mexico. Quat. Sci. Rev. 8:75–100.

CHOLNOKY, B. J. 1968. Die Okologie der Diatomeen in Binnengewassern. Cramer, Lehre. 699p.

EUGSTER, H. P. AND L. A. HARDIE. 1978. Saline Lakes. Pp. 237–293 *in* Lakes: Chemistry, Geology and Physics, A. Lerman ed., Springer-Verlag, New York. 363 pp.

FRITZ, S. C. AND R. W. BATTARBEE. 1988. Sedimentary diatom assemblages in freshwater and saline lakes of the northern Great Plains, North America: Preliminary results. Pp. 265–271 *in* Proceedings of the 9th International Diatom Symposium, F. E. Round, ed. Biopress Ltd., Koeltz Scientific Books, Bristol, Koenigstein.

GASSE, F. 1986. East African Diatoms, Taxonomy, ecological distribution. Bibl. Diatomologica 11:1–201.

———. 1987. Diatoms for reconstructing palaeoenvironments and palaeohydrology in tropical semi-arid zones. Examples of some lakes from Niger since 12,000 BP. Hydrobiol. 154:127–163.

GASSE, F., J. TALLING, AND P. KILHAM. 1983. Diatom assemblages in East Africa: Classification, distribution and ecology. Rév. d'Hydrobiol. Trop. 16:3–34.

GOMEZ DE OROZCO, F. 1972. Cronicas de Michoacán. Biblioteca del Estudiarte 12. Mexico. U. N. A. M.

HECKY, R. E. AND P. KILHAM. 1973. Diatoms in alkaline, saline lakes, ecology and geochemical implications. Limnol. Oceanogr. 18:53–71.

HUSTEDT, F. 1930. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. *In* Kryptogamen-Flora von Deutschland, Österreich und der Schwiez, L. Rabenhorst ed. Band 7, Teil 1. Akademische Verlagsgesellschaft, Leipzig. 920 pp.

———. 1959. Die Kieselalgen Deutschlands Österreichs und der Schweiz. *In* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, L. Rabenhorst, ed. Band 7, Teil 2. Akademische Verlagsgesellschaft, Leipzig. 845 pp.

———. 1961–1966. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. *In* Kryptogamen-Flora von Deutschland, Österreich und der Sewiz, L. Rabenhorst, ed. Band 7, Teil 3. Akademische Verlagsgeselleschaft, Leipzig. 816 pp.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae 1 Teil: Naviculaceae. Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fischer, Jena. 876 pp.

———. 1988. Bacillariophyceae 2 Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fischer, Stuttgart. 585 pp.

METCALFE, S. E. 1985. Late Quaternary Environments of Central Mexico: a diatom record. D.Phil. thesis, University of Oxford, 565 pp.

———. 1988. Modern diatom assemblages in Central Mexico: the role of water chemistry and other environmental factors as indicated by TWINSPAN and DECORANA. Freshw. Biol. 19:217–233.

———. 1990. *Navicula elkab* O. Müller—a species in need of redefinition? Diatom Res. 5:419–423.

METCALFE, S. E., F. A. STREET-PERROTT, R. B. BROWN, P. E. HALES, R. A. PERROTT, AND F. M. STEININGER. 1989. Late Holocene human impact on lake basins in Central Mexico. Geoarchaeology 4:119–141.

MÜLLER, O. 1899. Bacillariaceen aus den Natronthälern von El Kab (Ober-Aegypten). Hedwigia 38:274–321.

PATRICK, R. AND C. W. REIMER. 1966. The Diatoms of the United States, Vol. 1. Monograph No. 13, Acad. Nat. Sci. Philadelphia. 688 pp.

———. 1975. The Diatoms of the United States, Vol. 2. Monograph No. 13, Acad. Nat. Sci. Philadelphia. 213 pp.

RICHARDSON, J. L., T. HARVEY, AND S. A. HOLDSHIP. 1978. Diatoms in the history of shallow East African lakes. Polskie Archiwum Hydrobiologii 25:341–353.

SCHOEMAN, F. R. AND R. E. M. ARCHIBALD. 1976–1980. The Diatom Flora of South Africa, Nos. 1–6. CSIR Special Report WAT 50. Pretoria.

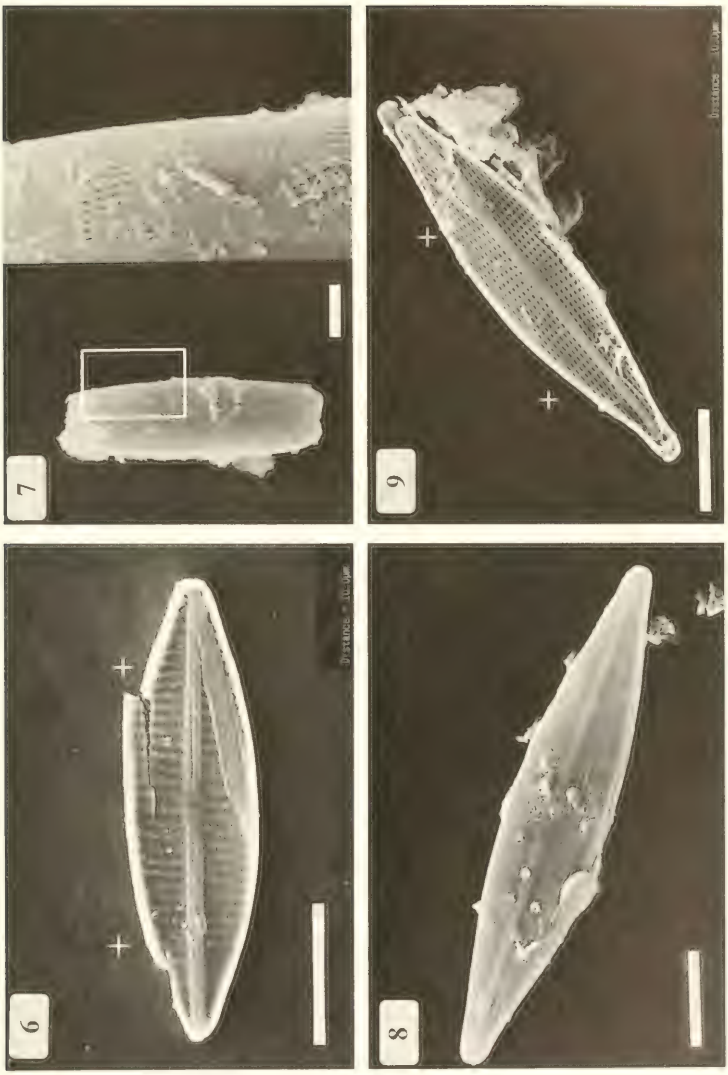
SECRETARÍA DE PROGRAMACION Y PRESUPUESTO. 1980. Sintesis Geografíca de Guanajuato. Mexico. 198 pp.

STUIVER, M. AND G. PEARSON. 1986. High precision calibration of the radiocarbon timescale, A. D. 1950 to 500 B. C. Radiocarbon 28:805–838.

Explanation of Plate

Plate 1, Figures 6–9

FIGURES 6–9. *Navicula elkab* O. Müller, examples from the La Piscina de Yuriria core. Scale bar = 5 μm.


7
9
6
8

Diatom-Stratigraphy in the Sediments of "Skua Lake," Horseshoe Island, Antarctic. Preliminary Report.

by

Anders Wasell

Department of Quaternary Research, University of Stockholm,
Odengatan 63, S-113 22 Stockholm, Sweden

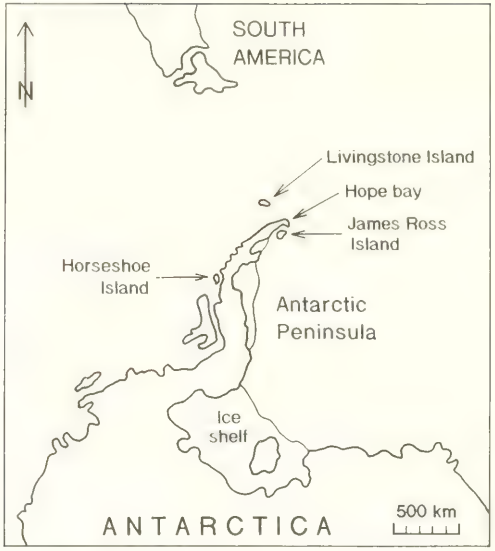
with 5 figures, 1 table, and 1 plate

Abstract: During the Swedish Antarctic expedition (SWEDARP 88/89) to the Antarctic Peninsula several lakes were cored and sampled for reconstruction of polar depositional environments. This is the first preliminary report from one of the investigated lakes: "Skua Lake," located at 67°48'40"S, 67°18'50"W, Horseshoe Island. The lake level is ca. 3.5 m a.s.l., and the surface area is c. 0.025 km^2. Several short cores (50–80 cm) were obtained from the lake. One of the longest cores was described and sampled in the field, and diatom assemblages have been analyzed approximately every 6 cm. The lowermost part between 80 and 50 cm shows a presence of marine diatoms, both neritic and sea ice species. The start of limnic conditions in the sediment core (20–0 cm) is marked by a peak in the frequencies of *Gomphonema angustatum* (Kützing) Rabenhorst, *Cocconeis japonica* (Hustedt) A. Cleve, and *Fragilaria virescens* Ralfs. Problems connected with radiocarbon datings are discussed.

Introduction

As part of the research project "Diatoms and Other Silica Particles in Polar Depositional Environments," this is the first preliminary report from one of the lakes investigated on the Antarctic Peninsula (Fig. 1). The goal of the project is to reconstruct and compare polar depositional environments and to trace indications of environmental and climatic changes. Studies within the project concentrate on siliceous microfossils and other particles preserved in the sediments, ice, or present in the water. Diatoms, phytoliths, and volcanic ash are the main objects of study. The origin, composition, and properties of biogenic and volcanic silica will also be included in the studies.

During the Swedish Antarctic expedition (SWEDARP 88/89) a number of lake sediment cores were collected from the Antarctic Peninsula and on adjacent islands (Fig. 1). The fieldwork was carried out in collaboration with Svante Björck (University of Lund), Kerstin Nordström (University of Uppsala), and Rolf Zale (University of Umeå) (Björck et al. 1990).



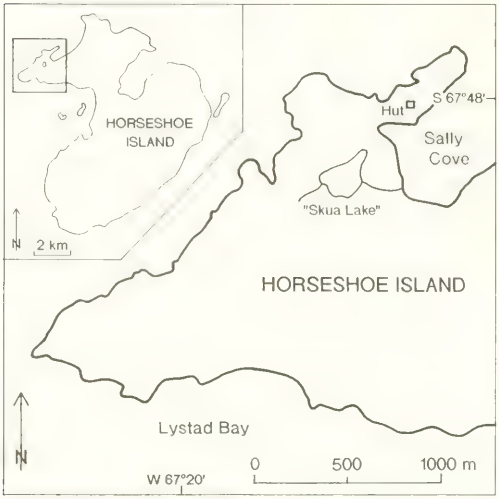


FIGURE. 1. (top) Locations of sampling sites. FIGURE 2. (bottom) "Skau Lake," Horseshoe Island, Antarctica.

"Skua Lake" (67°48'40"S, 67°18'50"W) is situated just (ca. 500 m) southwest of the BAS (British Antarctic Survey) hut at Sally Cove, Horseshoe Island (Figs. 2, 3). The lake level is c. 3.5 m a.s.l., and the surface area is about 0.025 km^2. The pH was measured in the surface water to be 6.6. The shoreline of the lake is stony and the surrounding ground gently sloping. The vegetation found around the lake consisted only of a few crustose lichens. At the time of the investigation (March 1989) the lake was fed by four snow patches and drained through a well-defined outlet into Sally Cove.

Materials and Methods

The sediments were cored in the deepest part (1.2–1.5 m) of the lake with two conventional Russian peat corers (5 and 10 cm diameter) (Jowsey 1966) and with one modified corer of the Livingstone type (Livingstone 1955; Zale and Karlén 1989). Complementary surface sediment samples were taken by a Benell sampler (Aaby and Digerfeldt 1986). There was no ice-cover on the lake, and the work was carried out from a small rubber boat.

Several short cores (50–80 cm) were obtained from the lake (Fig. 4). They all showed the same sequence measured from the top of the sediment surface. One of the longest cores was described and sampled in the field. Subsamples were taken each centimeter from this core; however, material from every sixth centimeter has been analyzed to date. Material for light microscopy was prepared by the method described by Batterbee (1986). The diatom floras of Hustedt (1930), Cleve-Euler (1951–1955), Hendey (1964), and Krammer and Lange-Bertalot (1986, 1988) have been used both for identification and ecological information. In this preliminary report results of diatom analysis, organic carbon content, and some ^{14}C dates are given. Between 200 and 800 diatoms were counted in every sample and both *Fragilaria* species and resting spores of *Chaetoceros* spp. and *Thalassiosira* spp. are included in the calculations. Some diatoms are abundantly and consistently present, others are present only as single occurrences at various levels of the cores. Therefore, only 16 taxa were chosen as representatives in the main diagram, while the rest are included in Other (Fig. 5). Some of the taxa encountered are shown in Figure 6.

Results and Discussion

The sediment cores could be divided in three litho-stratigraphical parts from the top of the surface-sediment:

(1) 0–17 cm gyttja, silty, greyish with an abundance of algal-flakes (mainly of the blue-green alga *Phormidium*).

(2) 17–40 cm silt, sandy, dark grey including some clay and some organic matter.

(3) 40–80 cm silt, clayey, slightly organic, dark grey.

As can be seen from Figure 5, the 80 cm length of the core can be divided in three major diatom zones: the lower part is dominated by marine diatoms and the upper part by freshwater species. In the middle part *Fragilaria pinnata* Ehrenberg is the most abundant species. Hustedt (1938) and Håkansson (1989) report that *Fragilaria* species live in shallow water, in the littoral zone. This may indicate the beginning of the isolation of "Skua Lake" from the sea. At about 18 cm the number of *F. pinnata* decreases and freshwater species common in shallow water, such as species of the genera *Achnanthes* and *Cocconeis*, increase. As already mentioned above, this is only a preliminary report, and more detailed analyses of diatom stratigraphy (every second centimeter), measurements of water content

FIGURE 3. "Skua Lake." Horseshoe Island, Antarctica (March 1989).

FIGURE 4. Sediment cores from "Skua Lake."

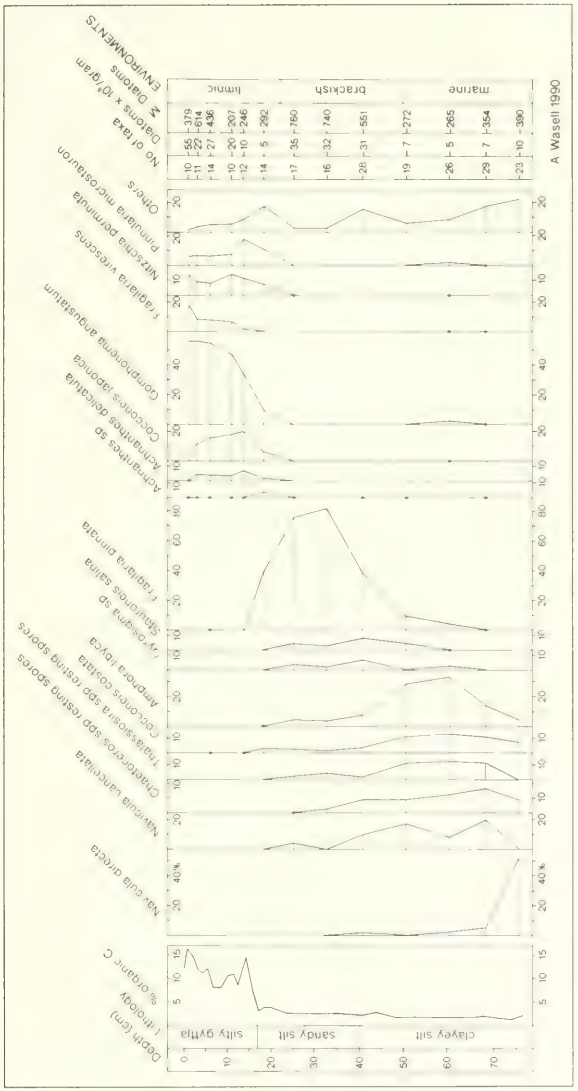


FIGURE 5. Diatom stratigraphy from "Skau Lake," Horseshoe Island, Antarctica. (• < 1 %.)

and biogenic silica, and morphological studies of several diatoms that caused difficulties in identification will be undertaken.

Radiocarbon datings of the sediment samples are shown in Table 1. Two obvious problems, however, seem to be connected with these datings. (1) The age of the recent material (blue-green algal flakes from the lake shore) is 120 yrs BP, which could mean that the nuclear bomb effect is missing or that the nuclear bomb effect is overridden by the marine reservoir effect. (2) The large differences in age between samples 14–18 cm (3170 yrs BP) and 9–13 cm (1440 yrs BP) could be explained by the marine effect on 14–18 cm but not on 9–13 cm, or by lack of sediment. Further discussions of the radiocarbon dating problems in "Skua Lake" and other lakes on the Antarctic Peninsula is presented in Björck et al. (in press).

Additional, detailed investigation will give a better explanation to the ecological history in these cores from "Skua lake."

TABLE 1. Radiocarbon dated samples from "Skua Lake," Horseshoe Island, Antarctica.

Material	Depth below sediment surface (cm)	14 C age yrs. BP	Lab . no.
Algal flakes	Lake shore	120 ± 45	Lu-3100
Sediment	9–13	1440 ±50	Lu-3143
"	14–18	3170 ± 90	Lu-3144
"	22–27	3160 ± 60	Lu-3099
"	27–30	3440 ± 110	Lu-3098

Acknowledgements

I would like to thank SWEDARP (Swedish Antarctic Research Programme), which organized the expedition; my colleagues in the field; and Britta Hörnström and Urve Miller of the Department of Quaternary Research, Stockholm University, for valuable support.

Literature Cited

AABY, B. AND G. DIGERFELDT. 1986. Sampling techniques for lakes and bogs. Pp 181–194 *in* Handbook of Holocene Palaeoecology and Palaeohydrology, B. E. Berglund, ed. John Wiley & Sons Ltd.

BATTARBEE, R. W. 1986. Diatom analysis. Pp 527–570 *in* Handbook of Holocene Palaeoecology and Palaeohydrology, B. E. Berglund, ed. John Wiley & Sons Ltd.

BJORCK, S., K. NORDSTROM, A. WASELL, AND R. ZALE. 1990. Holocene environmental land climatic changes around the Antarctic Peninsula based on lake sediment analyses. Pp 81–97 *in* Swedish Antarctic Research Programme 1988/89, A Cruise Report, A. Karlqvist, ed. Gotab, Stockholm.

BJÖRCK, S., C. HJORT, O. INGOLFSSON, AND G. SKOG. In press. Radiocarbon dates from the Antarctic Peninsula region—problems and potentials. J. Quat. Sci. 5.

CLEVE-EULER, A. 1951. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensakad. Handl. Fjärd Serien 2:1–163.

———. 1952. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensakad. Handl. Fjärd Serien 3:1–153.

———. 1953a. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensakad. Handl. Fjärd Serien 4:1–158.

———. 1953b. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensakad. Handl. Fjärd Serien 5:1–225.

———. 1955. Die Diatomeen von Schweden und Finnland. K. Svenska Vetensakad. Handl. Fjärd Serien 5:1–232.

HÅKANSSON, H. 1989. Diatom succession during Middle and Late Holocene time in Lake Krageholmssjön, southern Sweden. Nova Hedwigia 48:143–166.

HENDEY, N. 1964. An introductory account of the smaller algae of British coastal waters Part V. Bacillariophyceae (Diatoms). Fish. Inv., Ser. 4. Her Majesty's Stationery Office, London.

HUSTEDT, F. 1930. Bacillariophyta (Diatomeae). Heft 10. *In* Die Süsswasserflora Mitteleuropa, A. Pascher, ed. Fischer, Jena. 468 pp.

———. 1938–39. Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali und Sumatra nach dem Material der Deutschen Limnologischen Sunda-Expedition. Arch. Hydrobiol. Suppl. XV:131–177, 187–295, 393–506, 638–790; XVI:1–155, 274–394.

JOWSEY, P. C. 1966. An improved peat sampler. New Phytol. 65:245–248.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae. Teil 1. Naviculaceae. *In* Süsswasserflora von Mitteleuropa. Band 2, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds. Fisher, Stuttgart. 876 pp.

———. 1988. Bacillariophyceae. Teil. 2. Bacillariophyceae, Epithemiaceae, Surirellaceae. *In* Süsswasserflora von Mitteleuropa pa. Band 2., H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds. Fischer, Stuttgart. 596 pp.

LIVINGSTONE, D. A. 1955. A lightweight piston sampler for lake deposits. Ecology 36:137–139.

ZALE, R. AND W. KARLÉN. 1989. Lake sediment cores from the Antarctic Peninsula and surrounding islands. Geografiska. Annales 71A:211–220.

Explanation of Plate

Plate 1, Figures 6:1–6:15

FIGURE 6. Some of the diatom species from the sediment of "Skua Lake," Horseshoe Island. Scales = 5 µm. FIGURE 6:1. *Navicula directa* W. Sm. FIGURE 6:2. *Cocconeis costata* Greg. FIGURE 6:3. *Achnanthes delicatula* (Kützing) Grun. FIGURE 6:4. *Pinnularia microstauron* (Ehrenberg) Cleve. FIGURE 6:5. *Achnanthes* sp. FIGURE 6:6. *Amphora libyca* Ehrenberg FIGURE 6:7. *Stauroneis salina* W. Sm. FIGURE 6:8. *Navicula cancellata* Donk. FIGURE 6:9. *Gomphonema angustatum* (Kütz.) Rabn. FIGURE 6:10. *Fragilaria virescens* Ralfs. FIGURE 6:11. *Nitzschia perminuta* (Grun.) M. Perag. FIGURE 6:12–13. *Fragilaria pinnata* Ehrenberg FIGURE 6:14–15. *Cocconeis japonica* (Hust.) A. Cl.

6:1

6:2

6:3

6:4

6:5

6:6

6:8

6:7

6:9

6:10

6:11

6:12

6:13

6:14

6:15

Environmental Implications of the Late Quaternary Diatom History from Xingyun Hu, Yunnan Province, China[1]

by

Thomas J. Whitmore and Mark Brenner

Department of Fisheries and Aquatic Sciences, University of Florida
Gainesville, Florida 32606

and

Song Xueliang

Yunnan Institute of Geological Sciences, Baita Road, Kunming 650011
Yunnan Province, China

with 7 figures

Abstract: Xingyun Hu is a large, shallow lake on the Yunnan Plateau in southern China. ^{14}C dates indicate that an 8.4-m sediment core from Xingyun Hu represents a complete record of deposition from the Late Pleistocene (10,000 BP) to Present. Diatom analysis reveals three episodes of low-water level. Benthic diatoms dominate at 8.0–7.6 m and at 5.6 m in the sediment core indicating two low-water periods during the Pleistocene. In wetter Pleistocene periods, *Cyclotella radiosa* and other phytoplankton dominate. Non-carbonate clastic deposits change to carbonate-rich sediments at 5.0 m, which approximates the Pleistocene-Holocene boundary. Sedimentary organic matter reaches a maximum of 16.2 % at 4.0 m, which together with benthic diatoms suggest lower water with possible macrophyte proliferation. This inference of a drier Early Holocene is consistent with palynological evidence from other Yunnan lakes. Deeper water returns above 3.6 m, and *Cyclostephanos tholiformis* progressively replaces *Cyclotella radiosa*, *Aulacoseira* spp., and *Stephanodiscus* spp., indicating recent cultural eutrophication. As in other Yunnan lakes, diatoms are very sparse in the iron-rich clays and silts of the uppermost sediments. These deposits accumulated over the last several centuries and resulted from erosion accelerated by deforestation, agriculture, and lake-bottom reclamation. Trophic state has been historically high in Xingyun Hu, and changes in lake level rather than trophic state have been the primary determinant of benthic versus planktonic community dominance.

[1] Journal Series No. R-03504 of the Florida Agricultural Experiment Station.

Introduction

The Yunnan Plateau is a karst lake district in southwest China. The region has been subject to considerable anthropogenic influence in recent millennia, but the historical effects on the region's lakes are poorly known. Yunnan Plateau lakes compose one of the five principal lake districts in China. Most lakes in the province are shallow bicarbonate-type lakes formed by solution and/or tectonic processes. Dianchi, for example, is an economically important lake for the provincial capitol of Kunming. It is the largest Yunnan lake with an area of 305 km^2, but a maximum depth of only 8 m. Fuxian Hu, in contrast, is a fracture-fault lake with a maximum depth of 155 m. It is reported to be the second-deepest lake and to have the largest water volume of any lake in China (Ley et al. 1963; Liang and Cuo 1989).

Although Neolithic settlements near Yunnan lakes are reported from 10,000 B.P., the period of greatest cultural impact was after 1740 B.P. when terraced fields and irrigation were introduced to the area (Sun et al. 1986). Many lakes have been used for irrigation, and cores from four lakes, Cao Dian Hai, Yue Hu, Chang Hu, and Qing Shui Hai possess indurated, non-lacustrine deposits that suggest dryness in recent times due to climatic or human influence (Brenner et al. 1991).

Sun et al. (1986) report that drought caused Dianchi to become dry in 186 B. P. Dianchi's area has also been significantly reduced by alluviation and flood control measures that permitted land reclamation for agricultural purposes (Sun et al. 1986).

We observed lake-level management structures at Qilu Hu, where a canal and weir have been used to regulate drainage of this lake into a large, nearby sinkhole. Drawdown exposed riparian areas that were built up for agriculture with dredged sediment and terrestrial soil. Similar riparian agricultural methods are employed at Xingyun Hu.

Most work on lake sediments from Yunnan Province has been concerned with palynological reconstructions of long-term vegetational history in the region (e.g., Liu et al. 1986; Lin et al. 1986; Sun et al. 1986). Sun et al. (1986) did not find clear palynological evidence for historical anthropogenic effects on the Yunnan vegetation, though agriculture is now ubiquitous in the region, and natural vegetation is restricted to alpine and subalpine areas (Li and Walker 1986). Sedimentary evidence from Dianchi indicates that Late Pleistocene climatic conditions in Yunnan Province were cooler and wetter than at present (Sun et al. 1986; Lizhong et al. 1990).

The only paleolimnological studies in Yunnan were done on Qilu Hu in Tonghai County (Deevey et al. 1988; Brenner et al. 1991). An 11-m sediment core from Qilu Hu has a basal ^{14}C age of 30,960 860 B.P. Diatoms and aquatic pollen revealed that after 11,790 B.P., shallow-water conditions prevailed and probably reflect a drier Holocene climate. In Qilu Hu and four other Yunnan lakes from which we retrieved short cores, recent sediments consist of eroded silts and clays resulting from riparian agriculture. We extended our paleolimnological study to Xingyun Hu to determine if Qilu Hu's historical ecology typifies long-term ecological patterns in the shallow lakes of Yunnan Province.

The Study Site

Xingyun Hu, or Starcloud Lake, is a large (39.0 km^2), shallow lake (z_{max} = 12 m) that lies on the Yunnan Plateau of southwestern China at 24°20' N latitude, 102°45' E longitude, 90 km south of Kunming (Fig. 1). The lake is located 1723 m above msl and receives input from small, intermittent rivers near the village of Jiancheng. Xingyun Hu drains northeastward into Fuxian Hu via the channelized Gehe River and eventually into the Nanpan River system. The lake is 10.5 km long, 3.8 km wide, and has a watershed

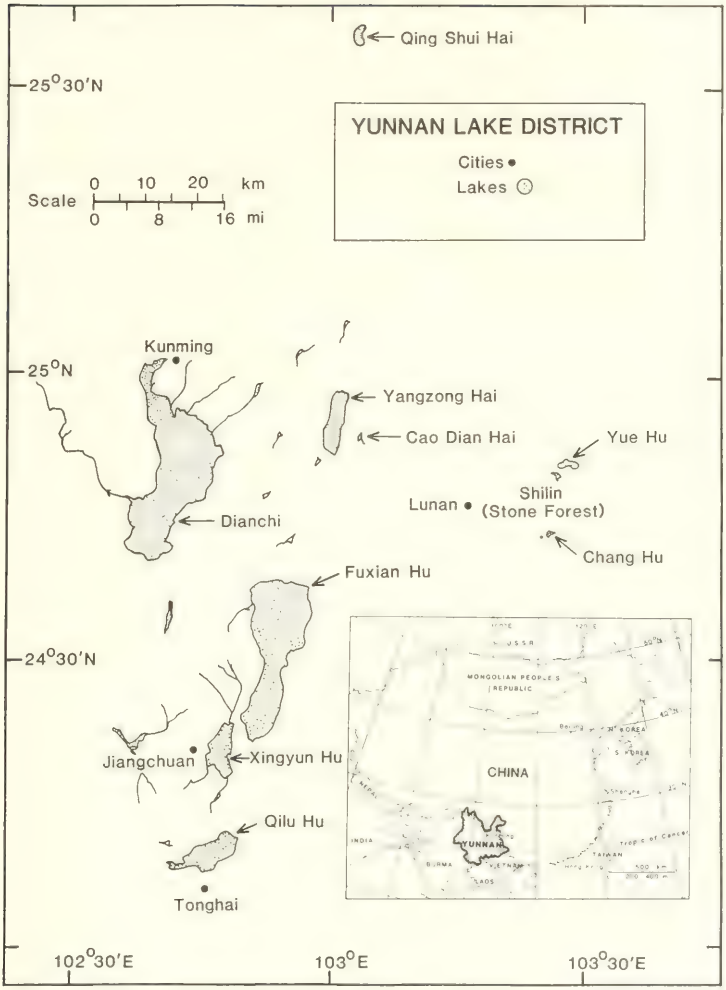


FIGURE 1. Map of the Yunnan Lake District showing the study lake, Xingyun Hu. Inset shows the location of Yunnan Province in southwest China.

of approximately 325 km^2. The village of Jiangchuan lies on the western shore of the lake. Erosion is visible on the highly agriculturalized and terraced hills surrounding Xingyun Hu, and steep, eroded slopes abut the lake on the eastern shore. Extensive reclaimed areas on the north and western shores support rice and other crops.

Xingyun Hu water is fresh (conductivity = 350 $\mu S\ cm^{-1}$). pH is generally 8.4–8.7 (Ley et al. 1963), although we recorded a high pH (8.82) in surface waters at 1540 hours on 6 July 1990 that probably reflected algal uptake of CO_2. We observed a Secchi depth of 2.4 m in July 1990, though transparency more typically ranges 50–60 cm in depth (Ley et al. 1963).

Materials and Methods

A 90-cm sediment core was retrieved from Xingyun Hu with a 4-cm diameter piston corer on 3 March 1989. The core was sampled in 2-cm increments and stored in plastic bags. A long sediment core was retrieved on 4 March 1989 using a steel-barrel Wright square-rod corer (Wright et al. 1984). This core began 0.6 m below the sediment-water interface and was retrieved in approximately 1-m segments to a total depth of 8.4 m in the sediment. Segments were extruded horizontally and subsampled at 0.2-m intervals.

Seventeen samples at approximately 0.5-m intervals were digested for diatom analyses using hydrogen peroxide and potassium dichromate (Van der Werff 1955). The top-most sample (0–2 cm) was obtained from the short core, whereas the remaining samples were taken from the long core. Samples were repeatedly rinsed with deionized water, settled, and aspirated until the dichromate color disappeared. Samples were then mounted on glass slides using Hyrax mounting medium, and a minimum of 300 diatom valves were counted and identified in each sample. Taxonomically difficult diatoms were studied using an Hitachi S-145A scanning electron microscope.

Total C was measured with a Coulometrics Inc. Model 5011 coulometer (Huffman 1977) and a System 120 preparation line at 950° C. Inorganic (carbonate) C was assayed by coulometry using a System 140 preparation line. Carbonates were estimated assuming all inorganic carbon was bound as $CaCO_3$. Organic C was calculated by difference between total and inorganic carbon. Total N and P were measured by autoanalyzer following digestion (Parkinson and Allen 1975). Radiocarbon dates were obtained from organic matter in bulk sediment samples by the Radiocarbon Laboratory at the University of Pittsburgh's Applied Research Center.

Results

The Xingyun Hu profile is divisible into three stratigraphic zones that correlate well with deposits from nearby Qilu Hu (Fig. 2). The lower zone consists of gray clay below 5.0 m that is principally non-carbonate clastics, with carbonates generally comprising < 1% by weight. Organic matter in this zone is < 10 % of the proximate composition. The middle zone extends from 5.0 m to 2.7 m depth. Deposits in this zone possess higher organic matter content and are carbonate-rich. Organic matter reaches a maximum of 16.2% dry weight at the 4.0-m level. The uppermost zone spans from 2.7 m to 0.0 m depth, and is composed of iron-rich red clays and silts that are low in organic matter and carbonates (Fig. 2). Mean percent organic C in the middle zone (6.61 ± 1.19) is higher than the means for the bottom (2.31 ± 0.94) and top (1.67 ± 0.86) zones. Total N shows a higher mean percentage in the middle zone (0.442 ± 0.054) than in the lower (0.162 ± 0.060) and upper (0.133 ± 0.063) zones. The high correlation between total N and organic C ($r = 0.973$, $p < 0.001$) suggests that virtually all sedimentary N is bound in organic matter.

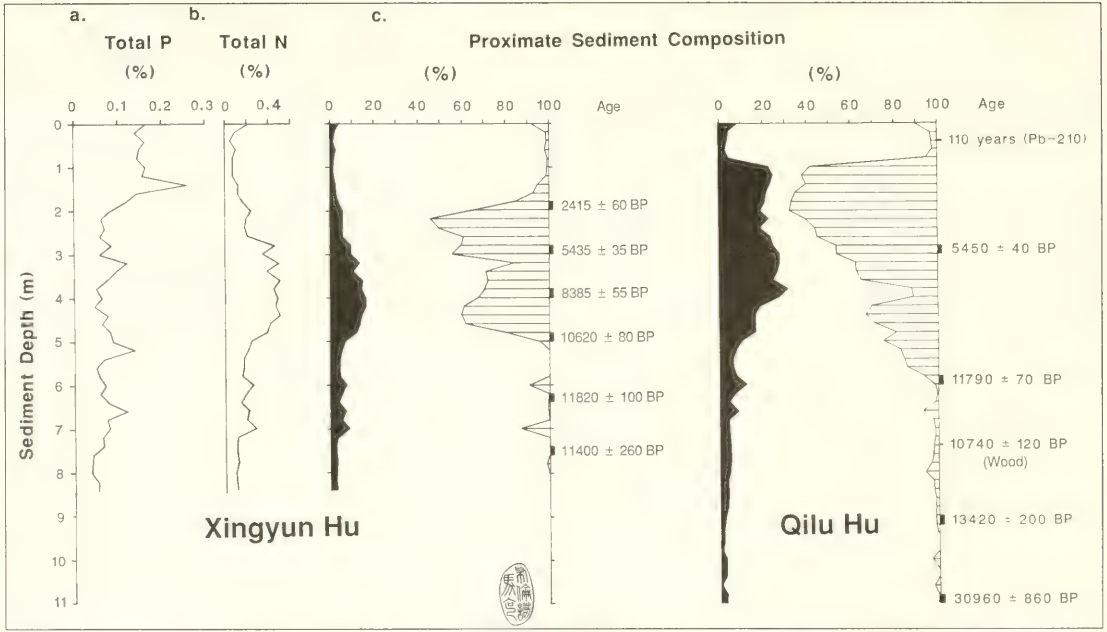


FIGURE 2a. Total P in the Xingyun Hu core. 2b. Total N in the Xingyun Hu core. 2c. Proximate sediment composition of long cores from Xingyun Hu and Qilu Hu. Blackened area on the left represents organic matter content, calculated as 2 x $C_{organic}$. Horizontal bars at the right represent carbonates (as $CaCO_3$), calculated as 8.33 x $C_{inorganic}$. The balance of the sediment is non-carbonate inorganics composed primarily of iron oxides and alumino-silicate clasties. ^{14}C dates were run on the organic fraction of bulk mud except the 10740 ± 120 date for Qilu Hu, an accelerator date on wood. ^{210}Pb date is 110 years before 1987.

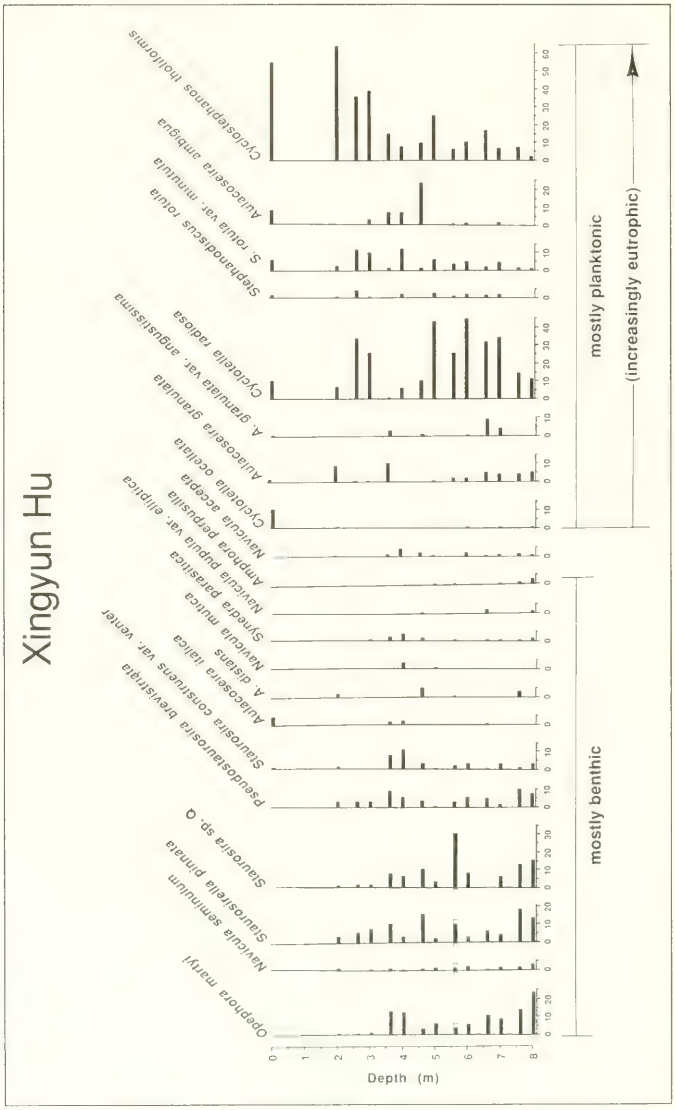


FIGURE 3. Percentage diagram of diatoms in Xingyun Hu sediments. Taxa shown represent > 2 % of flora in at least one level of core. Diatoms are absent in 1.6–0.6 m samples, inclusive.

Mean percent total P above 2.0 m (0.160 ± 0.038) is about twice the mean value for all levels below (0.074 ± 0.034). P in the upper zone apparently is adsorbed to recently sedimented alluvial silts and clays introduced by human disturbance.

^{14}C-dated deposits from Xingyun Hu (Fig. 2) indicate that the 8.4 m of sediment represent 10,000 years of continuous deposition from the Late Pleistocene to the Present. Bulk sediment ^{14}C dates in the Xingyun Hu sediment core correlate very well with bulk sediment dates obtained at similar depths in the Qilu Hu core. A wood sample at 7.36–7.39 m depth in the Qilu Hu core revealed a hard-water lake error (Deevey and Stuiver 1964) of approximately 1800 years in bulk sediment ^{14}C dates from Qilu Hu. We anticipate that bulk sediment ^{14}C dates for Xingyun Hu are also approximately 1800 years too old because of the hard-water lake effect.

Diatom analysis reveals that the most abundant diatom in the Xingyun Hu flora between the 8.0 and 5.0 m levels is *Cyclotella radiosa* (Grun.) Lemmermann (Fig. 3), a eutrophic indicator (Hakánsson 1989). Other eutrophic indicators, such as *Cyclostephanos tholiformis* Stoermer, Håkansson & Theriot and *Aulacoseira ambigua* (Grun.) Simonsen are less abundant in this interval. Low water levels are suggested by a higher proportion of benthic taxa, especially *Staurosirella pinnata* (Ehrenberg) Williams & Round and *Opephora martyi* Hérib., between 8 and 7.6 m depth in the sediment core, and again at 5.6 m (Fig. 4). A small and possibly new benthic form, here designated *Staurosira* sp. Q, is abundant during these low water levels, and it reaches a maximum of 30.3 % at 5.6 m.

At the 4.6 m level, *Cyclotella radiosa* declines and is replaced in dominance by *A. ambigua* (Fig. 3). The decline in planktonic forms between 4.6 and 3.6 m (Fig. 4) suggests another drop in lake-water level. Benthic diatoms, especially *S. pinnata*, *Pseudostaurosira brevistriata* (Grun.) Williams & Round, *Staurosira construens* var. *venter* Ehrenberg, and *O. martyi* are common at 4.0 and 3.6 m.

Higher trophic state at the 3.6-m level is indicated by the increase in *Cyclostephanos tholiformis*, a eutrophic to hypereutrophic form (Stoermer et al. 1987), and an increase in the mesotrophic to eutrophic indicator *A. granulata* (Ehrenberg) Simonsen. The abrupt increase in the proportion of planktonic taxa at the 3.0 m level (Fig. 4) suggests a return of deeper water, and the proportion of plankton continues to increase from the 3.0 m level to 0.0 m. *Cyclostephanos tholiformis* increases rapidly above 3.0 m, and reaches a maximum of 64 % at the 2 m level, perhaps indicating the onset of cultural eutrophication. Diatoms are essentially absent in the anthropogenically derived clays between 1.6 and 0.6 m. *Cyclostephanos tholiformis* is the most abundant diatom found in the recent sediments of Xingyun Hu.

An alternative explanation for the observed changes in dominance between planktonic and benthic communities is that Xingyun Hu has undergone historical changes in trophic state rather than in water level. Periods of benthic dominance may represent lower trophic state events. We examined the trophic preference of diatom assemblages in the Xingyun Hu sediment core using trophic autecological classifications compiled by Whitmore (1989) and more recently supplemented by autecological information from various sources (e.g., Hakánsson 1989; Stoermer et al. 1987; Anderson 1990).

Figure 5a shows the percentages of diatoms in each trophic category for samples from the Xingyun Hu sediment core. The percentage of eutrophic individuals is high and ranges between 40 % and 72 % of the assemblages, while the hypereutrophic individuals range between 10 % and 34 % of the assemblages in most samples. The percentage of hypereutrophic diatoms is approximately 8 % at the 5.6 and 6.0-m levels, and 9 % at the 4-m level.

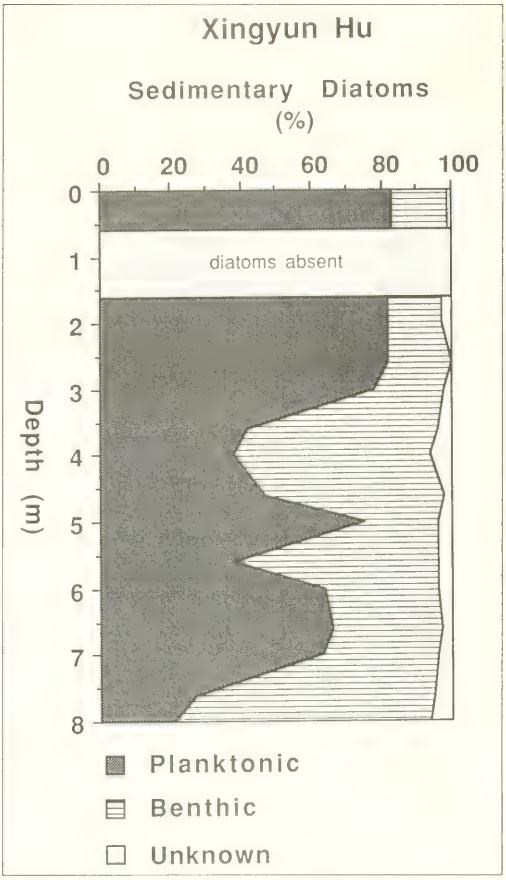


FIGURE 4. Benthic and planktonic percentages of diatom assemblages in the Xingyun Hu sediment core.

Brenner et al. (1993) constructed models for predicting limnetic total P values from a diatom/trophic index (Whitmore 1989) based on a calibration data set of 51 Florida lakes. Despite the geographic difference between Florida and Yunnan Province, lakes of these regions are ecologically similar because of their warm-temperate to subtropical locations, high insolation, shallow depths, karst edaphic settings, and often naturally high productivity. We apply our predictive model to the fossil assemblages from the Xingyun Hu sediment core. The modern limnetic total P value we infer from the 0–2 cm subfossil diatom assemblage is 0.198 mg l^{-1} P. Total P inferences for most levels in the sediment core are in the hypereutrophic range (> 0.100 mg l^{-1} P, Wetzel 1975). Inferences at some levels where benthic diatoms dominate are slightly lower. Total P inferences, for instance, at the 3.6-m (0.074 mg l^{-1} P) and 4.0-m levels (0.067 mg l^{-1} P) suggest eutrophic con-

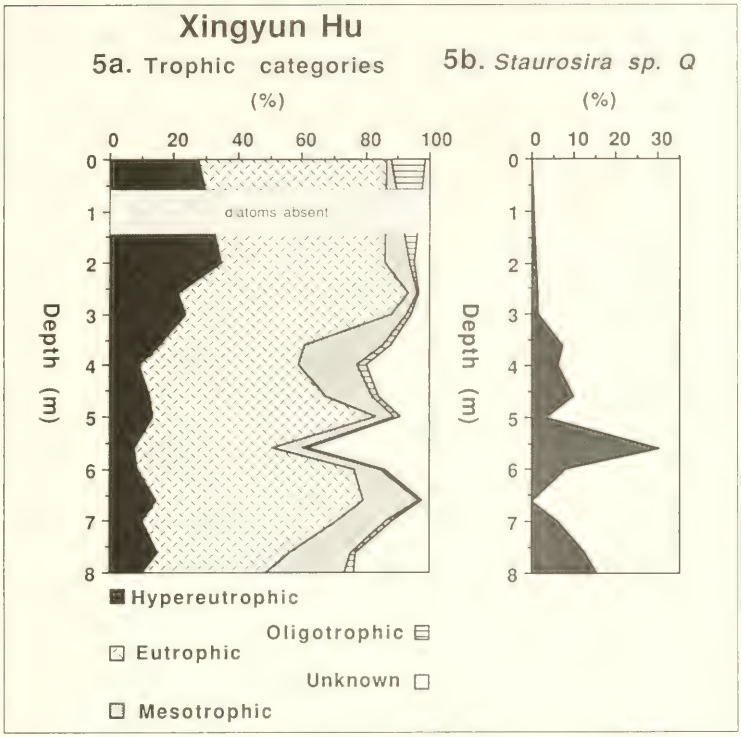


FIGURE 5a. Percentages of diatoms in various trophic categories in samples from the Xingyun Hu sediment core. FIGURE 5b. Percentage of *Staurosira* sp. Q in sediment core samples.

ditions, as do the inferences for the 7.6-m and 8-m levels (0.086 and 0.058 mg l^{-1} P, respectively).

Figure 5a shows that the percentage of diatoms with unknown trophic preference is high at some levels (38 % at 5.6 m, for example), which may affect total P inferences. Figure 5b shows, however, that most of the unknown ecological information is caused by a single taxon, *Staurosira* sp. Q (Fig. 7). This apparently undescribed taxon will probably be referred to the *S. construens* group (D. Williams and F. Round, personal communication), and may share the mesotrophic to hypereutrophic preferences of the taxa in that group (Whitmore 1989).

The percentages of diatoms in high trophic state categories in the Xingyun Hu core refutes the hypothesis of lower trophic state events. Our data for 53 Florida lakes shows that in mesotrophic lakes (0.010–0.030 mg l^{-1} total P), a mean of 2 % of the diatoms are generally hypereutrophic individuals, while the eutrophic, mesotrophic, and oligotrophic categories

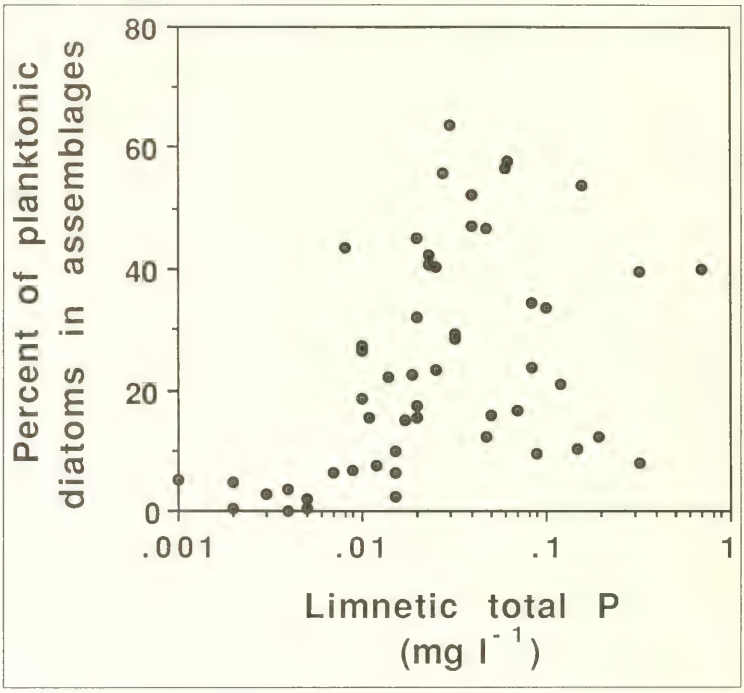


FIGURE 6. Limnetic total P versus the percentage of planktonic diatoms in recent surficial samples from 53 Florida lakes.

each have a mean of approximately 30 % of the remaining diatoms. In eutrophic lakes (0.030–0.100 mg l^{-1} total P), the mean percentage of diatoms in the hypereutrophic category is approximately 7 %, while eutrophic diatoms average 54 % of the assemblages. In hypereutrophic lakes, hypereutrophic diatoms average 19 % of the diatom assemblages, and eutrophic diatoms represent a mean of 53 %. For the 14 samples analyzed in the Xingyun Hu sediment core, a mean of 16.2 % of the diatoms had a hypereutrophic autecological preference, and 55.7 % of the diatoms were eutrophic forms. This strongly suggests that Xingyun Hu has been historically hypereutrophic.

The substantial increase in hypereutrophic taxa at 3.6 m and above (Fig. 5a) supports our interpretation of cultural eutrophication. The approximate 8 % mean of hypereutrophic diatoms and 53 % mean of eutrophic diatoms in the 5.6–6.0-m and 4-m levels suggests that these samples may represent eutrophic periods in the lake's development. Assignment of *Staurosira* sp. Q into lower trophic state categories would not alter the percentages of the higher trophic categories, and therefore would not change our interpretations. It is more likely, however, that *Staurosira* sp. Q exhibits a higher trophic state preference.

FIGURE 7. *Staurosira* sp. Q, an apparently undescribed taxon that may be referred to the *S. construens* group.

We examined the phenomenon of benthic versus phytoplankton dominance over the range of trophic states. A change from planktonic to benthic-dominated diatom assemblages is demonstrated by our set of 53 Florida lakes proceeding from higher to lower trophic state (Fig. 6). The shift to a benthic-dominated assemblage generally occurs, however, at oligotrophic conditions (0.010 mg l^{-1} total P) and below. Therefore, a change in trophic state is not a tenable explanation for the shifts observed in community lifeform preference

in Xingyun Hu. We retain our hypothesis that higher percentages of benthic taxa at the 3.6–4.6 m, 5.6 m, and 7.6–8.0 m samples are due to periods of lower water level.

Discussion

Xingyun Hu and Qilu Hu display similar sediment stratigraphies that reflect regional deposition patterns during the Late Quaternary. Shifts in proximate sediment composition indicate changing climate and anthropogenic influences. Late glacial deposits of both lakes are dominated by inorganic silts and clays. The dramatic change in sediment composition at about 5.0 m depth in the Xingyun Hu profile may indicate the Pleistocene-Holocene climatic transition. Unfortunately, the accurate location of the Pleistocene-Holocene boundary is uncertain because of hard-water lake effects on ^{14}C dates.

With the onset of warmer and drier climate about 10,000 B.P. (Sun et al. 1986), lacustrine productivity may have increased as suggested by the increase in *Aulacoseira ambigua* and *Cyclostephanos tholiformis* from 5.0 m to 4.6 m. Sedimentary deposits in Xingyun Hu contain an increasingly higher proportion of organic matter above 5.0 m. Carbonate content also increases and may reflect higher rates of biogenic marl precipitation. The drier climate induced lower water levels at the 4.0 m level, where the high proportion of benthic taxa and the peak in organic matter content may indicate that macrophytes temporarily played an important role in lake productivity. Macrophyte biomass is negatively correlated with phytoplanktonic biomass (Canfield et al. 1984) and limnetic total P (Whitmore 1991), and macrophyte proliferation during lower water levels might explain lower total P inferences we obtained in the 5.6-m, 6.0-m, and 4.0-m samples.

The increase in the proportion of planktonic diatoms above 3.6 m indicates that deeper water followed the dry period. *Cyclostephanos tholiformis* increases dramatically at the 2.0 m level, probably the result of human disturbance that caused a period of rapid eutrophication. This disturbance horizon is immediately followed by deposits of iron-rich silts and clays observed in both Xingyun Hu and Qilu Hu. These top-most deposits accumulated rapidly as a consequence of riparian soil erosion caused by deforestation and agriculture. Land reclamation activities also contributed to erosion and resuspension of littoral lake sediment.

By extrapolation of ^{210}Pb-based sedimentation rates from Qilu Hu, the uppermost silts and clays accumulated in the last 2–3 centuries. At Qilu Hu, the mean sedimentation rate during the last 110 years (0.14 g cm^{-2} yr^{-1}) exceeds the Early Holocene rate by nearly an order of magnitude (11,790–5,450 B.P. = 0.018 g cm^{-2} yr^{-1}). Recent clay deposits from Xingyun Hu are thicker than those measured at Qilu Hu, suggesting very high, modern sediment accumulation rates. Diatoms are virtually absent in these deposits due to dilution and/or breakage of valves. These uppermost muds are P-rich relative to deeper sediments indicating the recent trend toward cultural eutrophication and nutrient depletion of watershed soils.

Diatom evidence indicates that Xingyun Hu has been historically high in productivity since the lake Pleistocene. Many similarities exist between the diatom profiles of Xingyun Hu and Qilu Hu. As with Xingyun Hu, the Qilu Hu diatom profile shows a high trophic state assemblage during the Late Pleistocene, between 9 m and 6 m depth in the sediment core. This assemblage was principally a planktonic flora dominated by *Stephanodiscus rotula* (Kütz.) Hendey, *A. granulata*, *Cyclostephanos* cf. *dubius* (Fricke) Round, and *Cyclotella radiosa*. The Early Holocene dry period in Qilu Hu, between 5 m and 1 m depth in the core, is represented by a more persistent benthic assemblage that was dominated by *Staurosirella pinnata*, *Opephora martyi*, and *Staurosira* sp. Q. The greater

persistence of this benthic assemblage may be due to the shallower depth of Qilu Hu (z_{max} = 6.8 m) with respect to Xingyun Hu (z_{max} = 12.0 m). Low water level in Qilu Hu is corroborated by palynological evidence, especially pollen of *Alisma*, a macrophyte that grows emergent in shallow waters. Recent diatom assemblages in both Xingyun Hu and Qilu Hu are predominantly planktonic assemblages characteristic of deeper water and high trophic state.

Acknowledgements

This work was supported by NSF-INT grant 8802793. The Xingyun Hu core was collected by personnel from the Yunnan Institute of Geological Sciences. Frank Round, David Williams, Paul Zimba, and Eugene Stoermer helped with taxonomic identifications. Thanks to Matt Fisher for help with N and P analyses. Radiocarbon dates were provided by Robert Stuckenrath (Pittsburgh). Dan Engstrom ^{210}Pb-dated the Qilu Hu core. We thank Allen Moore and Dan Engstrom for limnological field assistance, and the Florida Museum of Natural History for use of facilities.

Literature Cited

ANDERSON, N. J. 1990. The biostratigraphy and taxonomy of small *Stephanodiscus* and *Cyclostephanos* species (Bacillariophyceae) in a eutrophic lake, and their ecological implications. Br. phycol. J. 25:217–235

BRENNER, M., K. DORSEY, SONG X., WANG Z., R. LONG, M. W. BINFORD, T. J. WHITMORE, AND A.M. MOORE. 1991. Paleolimnology of Qilu Hu, Yunnan Province, China. Hydrobiologia 214:333–340.

BRENNER, M., T. J. WHITMORE, M .S. FLANNERY, AND M. W. BINFORD. 1993. Paleolimnological methods for defining target conditions in lake restoration: Florida case studies. Lake and Reserv. Manage. 7:209–217.

CANFIELD, D. E., Jr., J. V. SHIREMAN, D. E. COLLE, W. T. HALLER, C. E. WATKINS, II, AND M. J. MACEINA. 1984. Prediction of Chlorophyll a concentrations in Florida lakes: importance of aquatic macrophytes. Can. J. Fish. Aquat. Sci. 41:497–501.

DEEVEY, E. S., M. BRENNER, A. M. MOORE, M. W. BINFORD, K. T. DORSEY, SONG X., WANG Z., AND HU Z. 1988. Paleolimnology and limnology of Qiluhu, Tonghai County, Yunnan: preliminary results. Journal of Yunnan University, 10 (suppl.):57–62.

DEEVEY, E. S. AND M. STUIVER. 1964. Distribution of natural isotopes of carbon in Linsley Pond and other New England lakes. Limnol. Oceanogr. 9:1–11.

HÅKANSSON, H. 1989. Diatom succession during Middle and Late Holocene time in Lake Krageholmssjön, southern Sweden. Nova Hedwigia 48:143–166.

HUFFMAN, E. W. D., JR. 1977. Performance of a new automatic carbon dioxide analyzer. Microchem. J. 22:567–573.

LEY S. H., YU M. K., LI K.C., TSENG C. M., CHEN C.Y., KAO P. Y., AND HUANG F. C. 1963. Limnological survey of the lakes of the Yunnan Plateau. Oceanol. Limnol. Sinica 5:87–114.

LI X. AND D. WALKER. 1986. The plant geography of Yunnan Province, southwest China. J. Biogeogr. 13:367–397.

LIANG D. AND CUO R. 1989. The distributions and hydrological characteristics of Yunnan Plateau lakes (abstract). Pp. 59–60 *in* Achievement in Research of Lake on Yunnan

Plateau Assembles for Thesis Abstract, Yang W. and Xie D., eds. Yunnan Environmental Science Institute and Yunnan Science and Technology Committee.

Lin S., Qiao Y., and D. Walker. 1986. Late Pleistocene and Holocene vegetation history at Xi Hu, Er Yuan, Yunnan Province, southwest China. J. Biogeogr. 13:419–440.

Liu J., Tang L., Qiao Y., M. J. Head, and D. Walker. 1986. Late Quaternary vegetation history at Menghai, Yunnan Province, southwest China. J. Biogeogr. 13:399–418.

Lizhong Y., F. Oldfield, Wu Y., Zhang S., and Xiao J. 1990. Paleoenvironmental implications of magnetic measurements on sediment core from Kunming Basin, Southwest China. J. Paleolimnol. 3:95–111.

Parkinson, J. A. and S. E. Allen. 1975. A wet oxidation procedure for the determination of nitrogen and mineral nutrients in biological material. Community Soil Sci. Plant Analysis 6:1–11.

Stoermer, E. F., H. Håkannson, and E. C. Theriot. 1987. *Cyclostephanos* species newly reported from North America: *C. tholiformis* sp. nov. and *C. costatilimbus* comb. nov. Br. phycol. J. 22:349–358.

Sun X., Wu Y., Qiao Y., and D. Walker. 1986. Late Pleistocene and Holocene vegetation history at Kunming, Yunnan Province, southwest China. J. Biogeogr. 13:441–476.

Van Der Werff, A. 1955. A new method of concentrating and cleaning diatoms and other organisms. Int. Ver. Theor. Angew. Limnol. Verh. 12:276–277.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia. 743 pp.

Whitmore, T. J. 1991. Diatoms as indicators of historical macrophyte biomass in Florida lakes. Ph.D. dissertation. University of Florida, Gainesville, Florida. 130 pp.

Wright, H. E., Jr., D. H. Mann, and P. H. Glaser. 1984. Piston corers for peat and lake sediments. Ecology 65:657–659.

Inferring Diatom Palaeoproduction and Lake Trophic Status from Fossil Diatom Assemblages

by

N. J. Anderson

Geobotany Division, Danish Geological Survey,
Thoravej 8, DK-2400 Copenhagen NV, Denmark

with 1 figure

Abstract: Whole-basin diatom accumulation rates (DARs) are presented for three lakes covering a range of trophic conditions and with diatom assemblages characteristic of variable water quality. The lakes have different perturbation histories: acidification, point-source eutrophication, and catchment disturbance (drainage-ditching). The whole-basin DARs increase as one would predict on the basis of the known ecology of the dominant diatoms, although the calculated DARs cover only ~two orders of magnitude ($0.85–10.6 \times 10^6$ cm^{-2} yr^{-1}). The implications of the data for inferences about lake trophic status are considered, and the possible relationship of DARs to weighted averaging inferred trophic status discussed.

Introduction

Inferring past changes in diatom productivity and lake trophic status from sediment diatom assemblages have been undertaken using a variety of methods (Battarbee 1986a). Many of these approaches make assumptions both about the relationship of diatom water column production to that of the whole system (i. e., the comparative importance of non-siliceous algae), as well as processes controlling the formation of the sediment assemblage (diatom taphonomy and sediment deposition; i.e., these factors are considered to be unimportant).

The interpretation of relative frequency diatom stratigraphy still relies heavily on an indicator species approach (cf. Stoermer 1984; Battarbee 1986a), and often vague, ill-defined, unquantified measures of diatom environmental tolerances and their productivity implications. This situation is, however, changing with the increased use of weighted averaging calibration to quantify chemistry and environmental tolerances of diatoms (Birks et al. 1991), and the possibility of its application to productivity measures (Christie and Smol 1990).

Diatom accumulation rates (DAR) offer an alternative and, theoretically, more rigorous approach to interpreting past diatom palaeoproduction, although they have their own problems (Battarbee 1978; Anderson 1989, 1990). However, DAR differences between lakes (of different trophic status) have not been evaluated, largely because relatively few

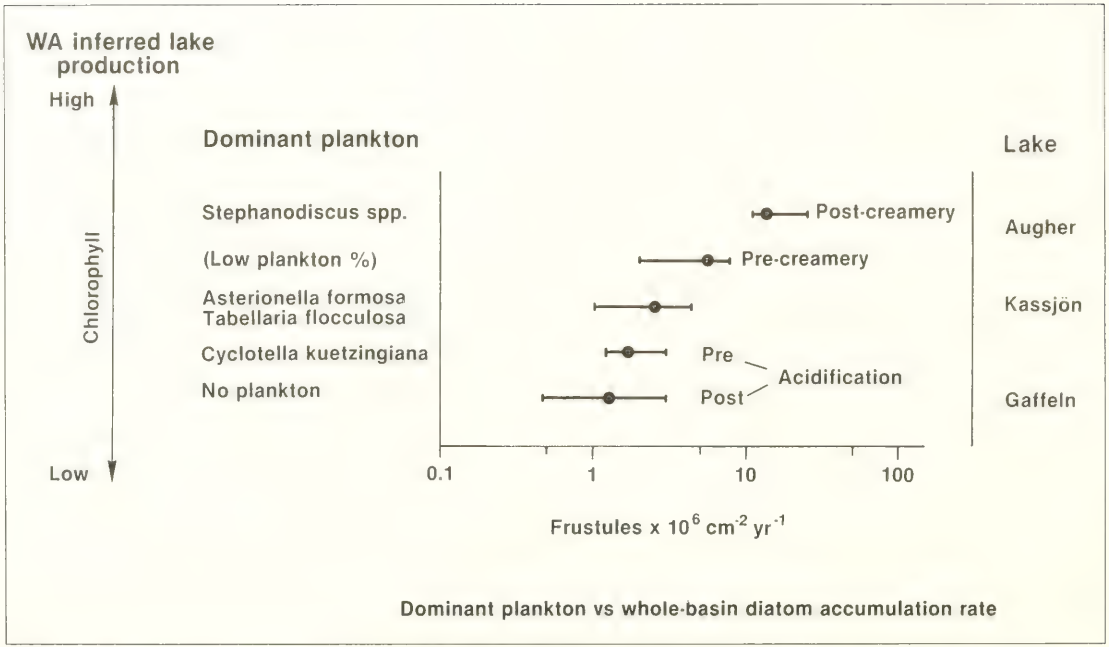


FIGURE 1. Mean whole-basin diatom accumulation rates plotted vs. dominant planktonic diatoms. The vertical axis: "inferred chlorophyll" is a hypothetical gradiant that may be inferred from diatom assemblages in surface sediment data sets using weighted averaging calibration methods. The vertical distribution of the lakes is: bottom, Gaffeln (acidification); middle, Kassjön (drainage ditching); top, Augher (point-source eutrophication).

workers calculate accumulation rates and because of the problem of comparing single cores between lakes. Similarly, it is difficult to compare whole-basin rates with one-core studies because of the possibility of considerable within-basin variation (Anderson 1990).

Summary results are presented here for three lakes for which a whole-basin accumulation rate has been calculated, and the implications for interpreting diatom stratigraphy in terms of diatom whole-lake palaeoproduction assessed.

Materials and Methods

Diatom sample preparation followed standard methodology (Battarbee 1986a) and concentration determined using the microsphere method (Battarbee and Keen 1982). Dating for calculation of diatom accumulation rates (DAR) at Gaffeln and Lough Augher was by ^{210}Pb (Anderson 1989; Anderson and Renberg 1992) and at Kassjön by varve counting. Whole-basin accumulation rates are arithmetic means of all cores. Where area weighted means have been calculated the differences between arithmetic and area-weighted means were felt to be small in relation to other error sources (e.g., concentration estimates, dating errors). Also, the error associated with whole-basin estimates and the difference between arithmetic and area-weighted means will decrease with the number of cores used (Anderson 1990). Means of pre- and post-disturbance DAR for the three lakes are presented where possible; the number of cores used to calculate these values varies accordingly.

Study Sites

All the study sites are small lakes but of varying water quality. Augher Lough (Co. Tyrone, N. Ireland) is a eutrophic lake (area 9.2 ha; max depth 14.5 m) polluted in the recent past by creamery effluent disposal. Pre-creamery (< 1900) and creamery (1940–1970) DARs are given. Kassjön (23 ha; max. depth 12.5 m) is a boreal forest lake in northern Sweden (Västerbotten) with ~75% of its catchment currently used for agricultural purposes. Between 1900 and 1902, parts of the catchment were drained by ditching, and an average accumulation rate for 1900–1988 is presented. Gaffeln (Bohuslän, SW Sweden) (6.2 ha, max. depth 15.5 m) is a strongly acidified lake (pH 4.6) that has lost both its fish populations and planktonic diatom flora. Pre-acidification (< 1900) and acidification (1950–1988) period DARs are given. Although water quality data are limited for the lakes, they conform reasonably well to the typically defined lake trophic gradient: oligotrophic (Gaffeln); mesotrophic (Kassjön); eutrophic (Augher).

Results and Discussion

The estimated mean whole-basin accumulation rates cover a range of values (0.85–10.6 $\times 10^6$ frustules cm^{-2} yr^{-1}; Fig. 1). The means increase as one would predict on the basis of the planktonic diatom flora and the known disturbance histories; apart, that is, from the acidified site. At the latter, acidification caused the loss of the planktonic diatoms but did not result in a reduction of total diatom production (Anderson and Renberg 1992). The ranges encountered for each lake illustrate clearly the problems of extrapolating from single cores to a basin-mean diatom accumulation rates; single cores are unlikely to be representative of the basin average (Anderson 1990). However, it should be recognized that these ranges include core locations that would not generally be used for palaeoecological study.

Floristics, Diatom Ecology, Accumulation Rates, and Inferred Productivity

Given even a qualitative approach to planktonic diatom ecology, it is reasonable to assume that lakes dominated by *Asterionella formosa* have higher productivities (and hence DAR)

than lakes with *Cyclotella kuetzingiana* as the dominant planktonic diatom (Hörnström 1981). Similarly, small *Stephanodiscus* species imply still higher productivity (Stoermer 1984), although in this case there is the possibility of system silica limitation (Battarbee 1986a; Anderson 1989).

The assumption here, of high *Stephanodiscus*-high lake (and diatom) production (high DAR), acid flora-low production (low DAR), works reasonably well in terms of these lakes (e.g., Gaffeln-Kassjön-Augher) (Fig. 1). They represent a productivity gradient (re-diatoms), both as calculated accumulation rates and in terms of diatom floristics and ecology. The estimated range of DAR values for the different lakes covers, however, only ~two orders of magnitude, whereas chlorophyll values for oligo-eutrophic range of lakes may commonly cover 3–4 orders (Dillon and Rigler 1974).

Despite, however, the rise of nutrient ratio competition theory (Tilham et al. 1982) and other models describing the growth and seasonal distribution of planktonic diatoms (and other phytoplankton in general), there are many taxa for which even descriptive autecological data are not available. For many benthic taxa, the situation is similar or worse, and although the pH surface-sediment data sets have refined pH and metal tolerances of many taxa (Birks et al. 1991), their association with nutrients are still unclear. Associations of species assemblages with lake trophic status will be refined as surface sediment data sets for more eutrophic lakes become available (e.g., Brugam 1983; Whitmore 1991).

The vertical axis in Figure 1—weighted averaging (WA) inferred chlorophyll—as yet remains unquantified, and as shown here the inferred gradient is a subjective one. In palaeolimnological terms the quantification of the y-axis should soon be possible if eutrophic lake calibration data sets fulfill their promise. A more rigorous appraisal of the relationship presented in Figure 1 (i.e., inferred chlorophyll vs. total diatom accumulation rate) would be to calculate whole-basin DARs for a range of lakes with contemporaneous phytoplankton and chemical data. Palaeolimnological study of phytoplankton monitored lakes would also permit an accurate estimation of diatom-loss processes prior to final burial (cf. Haworth 1980; Schindler 1987).

Diatoms and Inferred Epilimnetic Productivity

Calibration data sets for eutrophic lakes offer, through the use of WACALIB (Weighted Averaging Calibration; Line and Birks 1990; Birks et al. 1991), the possibility of reconstructing past levels of phosphorus and chlorophyll. Depending on the available water chemistry, the reconstructed parameters will largely relate to epilimnetic conditions. For extensive monitoring data sets it may be possible to assess the relationship between the surface diatom assemblage and spring mean chlorophyll (i.e., the period of main planktonic diatom contribution), summer (cyanobacteria and/or dinoflagellates), or the annual mean. The relationship of these values (spring, summer peaks vs. mean annual values) can vary substantially in different lake systems (Reynolds 1984). There are, therefore, considerable ecological implications for using reconstructed chlorophyll based on these different means.

As phosphorus loadings increase, however, the relative importance of diatoms may be reduced, due to either direct Si limitation (Battarbee 1986a; Oldfield 1977) or changing Si:P and N:P ratios (Tilman et al. 1986). These factors may account for the limited range in the DARs; the lake at the eutrophic end of the scale (Augher) may reflect silica limitation. The epilimnetic chlorophyll levels for this lake would probably reflect considerable blue-green, non-siliceous algal crops. Similarly, with acidification the loss of the planktonic diatoms is in part compensated for by increased chrysophyte and dinoflagellate production.

It is in these areas that the possibility of reconstructing epilimnetic chlorophyll will be most useful, both to the palaeolimnologist and for lake restoration strategies. As a management tool weighted averaging reconstructed chorophyll may be important as it is more readily interpreted by water engineers and applied limnologists than are diatom stratigraphies or accumulation rates.

Littoral Production

Epilimnetic chlorophyll concentration is a measure of phytoplankton biomass and does not consider the input of the littoral community (Wetzel 1979). The relationships between littoral and profundal production are not yet fully evaluated (Hansen 1990). Whole-basin DARs, however, include a benthic (periphytic) component, and to a certain extent therefore offer a measure of the relative importance of the benthic and littoral contributions to the whole-lake system.

Interpretation of relative frequency diatom stratigraphy usually concentrates on increases in planktonic taxa, which often results in reciprocal decreases in benthic taxa (Battarbee 1986b; Engstrom et al. 1985). As such, little can be said about the response of the attached and benthic taxa to eutrophication, for example, despite the importance of diatoms in littoral algal communities. While the use of DAR removes the problems of percentage data for interpreting the periphyton (Battarbee 1986b; Engstrom et al. 1985), it does not reflect their true response, because of spatially variable deposition (Anderson 1989, 1990) and greater retention of benthic taxa close to their source (Bradbury and Winter 1976). One would, intuitively, expect benthic diatom production to increase as nutrient loading increased, and whole-basin DARs tend to show this.

It is in this area of benthic palaeoproduction, that whole-basin DARs have proved beneficial (Anderson 1989; Anderson and Renberg 1992). Anderson (1989) recorded increased periphytic production to nutrient enrichment at Augher; while Anderson and Renberg (1992) showed how declines in benthic diatom accumulation rates in deep-water cores in the acidified lake Gaffeln, were an artefact of changed diatom deposition patterns associated with acidification. On a whole-basin basis, benthic DARs increased.

Calibration data sets reconstruct epilimnetic P and chlorophyll, which may be adequate for lake restoration programs and background data for routine monitoring, but may be inadequate for more ecologically slanted projects. Benthic taxa may not relate to the physico-chemical environment, but also to substrate and micro-habitat variables (Cox 1988), which are not easily quantifiable for inclusion in calibration data sets. The chemical environment of the littoral zone, macrophyte stands, and interstitial pore-waters, which are substantial source areas for diatoms that accumulate in the sediments, may not be clearly related to epilimnetic water chemistry.

What Do Diatom Accumulation Rates Represent?

It is important to consider why the Augher DAR is only ~10 times higher than Gaffeln. The relationship between the different DARs should not be over-interpreted until there has been a strict evaluation of the relationship between whole-lake productivity and diatom accumulation in the sediments (i.e., the burial efficiency of diatom production in small lakes; cf. Anderson 1989; Battarbee 1986a). The different whole-basin DAR may reflect differential loss processes between the lakes. There have been few comparisons of initial diatom production with sediment accumulation rates. Haworth (1980) found excellent temporal agreement between the phytoplankton records and sediment diatom assemblages in Blelham Tarn, and a reasonable relationship between total number of *Stephanodiscus* in the sediments and mean numbers in the overlying water column (Haworth 1979).

Loss Processes

Most diatoms produced in the water column of small lakes reach the sediments with minimal dissolution, unlike the oceans and deep lakes (Reynolds 1986, but cf. Sommer 1989). However, the relationship between lake production and diatom accumulation is influenced by a number of loss processes. The DARs (Fig. 1) may reflect these loss processes: grazing, washout, and dissolution.

While grazing can reduce population growth of planktonic diatoms, it generally has minimal impact on crops (Jewson et al. 1982; Reynolds 1984). The cessation of the spring diatom crop in temperate, monomictic lakes probably reflects other more important (to the diatoms) loss processes, especially Si limitation and increased sinking rates (Reynolds 1984). Small *Stephanodiscus* species often bloom at low water temperatures and light levels, prior to the late spring development of herbivores (Bradbury 1975).

If grazing of diatom crops is excessive, there are implications for both approaches to reconstructing past diatom production and lake trophic status. For the WA-calibration approach, if the structure of the diatom community and hence the diatom sediment assemblage is influenced strongly by grazing (i.e., grazing resistant colonial forms vs. readily grazed unicells), then the nutrient signal will be more difficult to determine. Grazing may cause underrepresentation of diatoms, because although the diatom frustule may survive gut passage intact, grazing commonly can cause fracturing, which enhances dissolution.

While plankton crops and sedimentation have been shown to be similar (Sommer 1984; Reynolds et al. 1982; Livingstone and Reynolds 1981), there is an obvious need for (post-burial) sediment accumulation rates (i.e., after dissolution and breakage and removal from the bioturbated front) to be calibrated against known water column production (Battarbee 1986a); that is, the burial efficiency to be estimated.

Washout and Dissolution

Another important loss process in small lakes may be washout. Although the retention time of Augher Lough is approximately five months, at the time of maximal diatom growth, flushing will probably be increased, thereby reducing the standing stock (Reynolds and Lund 1988). Battarbee (1978) calculated that in 1970 ~8% of the planktonic diatom crop was lost down the outflow in Lough Neagh. Sommer (1985) and Reynolds et al. (1982) reported underrepresentation of small centric diatoms when they compared maximal standing crops and number caught in sediment traps. The low dissolution kinetics quoted by Reynolds (1986) for even thin diatoms suggests that this discrepancy may be due to washout (in Windermere at least, Lake Constance has a four-year retention time) prior to final sedimentation (but cf. Sommer 1989).

It remains to be determined whether dissolution is uniform for a diatom crop after deposition at the sediment surface (cf. Jewson et al. 1981), or whether part of the crop is recycled, i.e., those that are eaten by benthic invertebrates and the frustule broken, thereby enhancing dissolution. In Lough Neagh, Batterbee (1978) reported large increases in lake Si concentrations of which inflow inputs could account for only < 20%, the difference attributable to sedimentary release (Rippey 1983). Despite the high Si release rate (Rippey 1983) in Lough Neagh, diatom concentrations are still on the order of $5–10 \times 10^7$ cells cm^{-3} ($2–4 \times 10^8$ cells g $(DW)^{-1}$) and preservation remains good (Battarbee 1978; Flower 1991).

In shallow calcareous and saline lakes' diatoms may be entirely absent or concentrations (and preservation quality) decrease down core (Fritz 1990). As dissolution in the water column of lakes is minimal, sediment dissolution is the more likely cause and may be

related to groundwater discharge continually reducing the Si concentration in the interstitial waters.

Implications and Conclusions

The complexities of diatom accumulation in lake basins, together with the relationship between algal floristics and trophic status does not bode well for quantitative inferences of lake trophic status (Oldfield 1977), unless the use of relative frequency data for inferring quantified palaeoproduction data (via transfer functions) overrides loss processes and variability problems (Whitmore 1991). Anderson (1989, 1990) found percentage data less variable than the quantitative data, but the interpretation of the accumulation data offered slightly contrasting (if complementary) views of the lake's history. The similarity of the mean DARs supports the use of a weighted averaging approach to palaeoproduction using relative frequency data (which are less prone to data loss, cf. Whitmore 1991). Whole basin DAR do, however, serve a useful purpose in closing the silicon cycle in lakes (Reynolds 1986).

Whitmore (1991) has argued that dissolution of diatom assemblages limits the usefulness of DARs, and that trophic-state parameters derived from relative frequency assemblages are a better measure of past lake trophic status. This is probably the case where preservation is bad and/or silicon limitation restricts the contribution of diatoms to whole-lake palaeoproduction. Where there is differential loss within a diatom assemblage, the resulting bias would also influence the surface sediment-water chemistry relationship.

It remains to be ascertained whether the differences obtained for these lakes (Fig. 1) reflect real productivity differences (due to different water column grazing, nutrient limitation, and competition) or differences in geochemical cycling of Si between lakes. Relationships between initial production and final sedimentation need to be clarified; there is a clear need for a calibration of whole-basin DAR at sites where there is either a Si-budget and/or suitable phytoplankton monitoring program.

Where diatom ecology is the main interest or preservation is adequate, whole-basin DARs have to be considered superior to either single core relative frequency data or accumulation rates, as they offer a more realistic insight to the differential contributions of plankton and periphytic diatoms. There is also a clear need for more than one core if meaningful comparisons are to be made between different lakes, or DARs are to be interpreted in terms of changing productivity.

Whole-basin studies also assist in our understanding of deposition processes and their influence on diatom assemblages and their role in the Si-cycle. Similarly, the role of trophic state inferences for water management and restoration programs will be considerable. However, to claim that reconstructed epilimnetic P or chlorophyll are whole-lake production indicators merely underplays the importance of the littoral zone (algae, macrophytes, and bacteria) in lake ecosystems.

Literature Cited

Anderson, N. J. 1989. A whole-basin diatom accumulation rate for a small eutrophic lake in Northern Ireland and its palaeoecological implications. J. Ecol. 77:926–946.

———. 1990. Variability of diatom concentrations and accumulation rates in sediments of a small lake basin. Limnol. Oceanogr. 35:497–508.

Anderson, N. J. and I. Renberg. 1992. A paleolimnological assessment of diatom production responses to lake acidification. Environmental Pollution 78:113–119.

BATTARBEE, R. W. 1978. Observations on the recent history of Lough Neagh and its drainage basin. Phil. Trans. R. Soc. B. 281:303–345.

———. 1986a. Diatom analysis in Berglund, B. E. (ed.) Pp. 527–570 *in* Handbook of Holocene palaeoecology and palaeohydrology. Chichester, Wiley.

———. 1986b. The eutrophication of Lough Erne inferred from changes in the diatom assemblages of 210Pb- and 137Cs-dated sediment cores. Proc. R. Irish Acad. B 86:141–168.

BATTARBEE, R. W. AND M. J. KEEN. 1982. The use of electronically counted microspheres in absolute diatom analysis. Limnol. Oceaongr. 27:184–188.

BRADBURY, J. P. 1975. Diatom stratigraphy and human settlement in Minnesota. Geol. Soc. Am. Special Paper 171.

BRADBURY, J. P. AND T. C. WINTER. 1976. Areal distribution and stratigraphy of diatoms in the sediments of Lake Sallie, Minnesota. Ecology 57:1005–1014.

BIRKS, H. J. B., S. JUGGINS, AND J. M. LINE. 1991. Lake surface-water chemistry reconstructions from palaeolimnological data. Pp. 301–313 *in* The Surface Waters Acidification Programme, J. B. Mason, ed. Cambridge University Press, Cambridge.

BRUGAM, R. B. 1983. The relationship between fossil diatom assemblages and limnological conditions. Hydrobiol. 98:223–235.

CHRISTIE, C. E. AND J. P. SMOL. 1990. Paleolimnological reconstructions of nutrient concentrations using diatom assemblages and weighted averaging techniques. Abstract. 11th International Symp. Living and Fossil Diatoms.

COX, E. J. 1988. Has the role of the substratum been underestimated for algal distributional patterns in freshwater ecosystems? Biofouling 1:49–63.

DILLON, P. J. AND F. H. RIGLER. 1974. The phosphorous-chlorophyll relationship in lakes. Limnol. Oceanogr. 19:767–773.

ENGSTROM, D. R., E. B. SWAIN, AND J. C. KINGSTON. 1985. A palaeolimnological record of human disturbance from Harvey's Lake, Vermont: geochemistry, pigments and diatoms. Freshw. Biol. 15:261–288.

FLOWER, R. J. 1991. Field calibration and performance of sediments traps in a eutrophic holomictic lake. J. Paleolimnol. 5:175–188.

FRITZ, S. C. 1990. Twentieth-century salinity and water-level fluctuations in Devils Lake, North Dakota: test of a diatom-based transfer function. Limnol. Oceanogr. 35:1771–1781.

HANSEN, L-A. 1990. Quantifying the impact of periphytic algae on nutrient availability for phytoplankton. Freshw. Biol. 24:265–273.

HAWORTH, E. Y. 1979. The distribution of a species of Stephanodiscus in the recent sediments of Blelham Tarn, English Lake District. Nova Hedwigia, Beih. 64:395–410.

———. 1980. Comparison of continuous phytoplankton records with the diatom stratigraphy in the recent sediments of Blelham Tarn. Limnol. Oceanogr. 25:1093–1103.

HÖRNSTRÖM, E. 1981. Trophic characterization of lakes by means of qualitative phytoplankton analysis. Limnologica 13:249–261.

JEWSON, D. H., B. RIPPEY, AND W. K. GILMORE. 1981. Loss rates from sedimentation, parasitism, and grazing during the growth, nutrient limitation, and dormancy of a diatom crop. Limnol. Oceanogr. 26:1045–1056.

LINE, J. M. AND H. J. B. BIRKS. 1990. WACALIB version 2.1–a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging. J. Paleolimnol. 3:170–173.

LIVINGSTONE, D. AND C. S. REYNOLDS. 1981. Algal sedimentation in relation to phytoplankton periodicity in Rostherne Mere. Br. phycol. J. 16:195–206.

OLDFIELD, F. 1977. Lakes and their drainage basins as units of sediment-based ecological study. Prog. Phys. Geog. 1:460–504.

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.

———. 1986. Diatoms and the geochemical cycling of silicon. Pp. 269–289 *in* Biomineralization in lower plants and animals, B. S. C. Leadbeater and R. Riding eds. Special volume of the Systematics Association 30. Clarendon Press, Oxford.

REYNOLDS, C. S. AND J. W. G. LUND. 1988. The phytoplankton of an enriched, soft-water lake subject to intermittent hydraulic flushing (Grasmere, English Lake District). Freshw. Biol. 19:379–404.

REYNOLDS, C. S., H. R. MORISON, AND C. BUTTERWICK. 1982. The sedimentary flux of phytoplankton in the south basin of Windermere. Limnol. Oceanogr. 27:1162–1175.

RIPPEY, B. 1983. A laboratory study of the silicon release process from a lake sediment. (Lough Neagh, Northern Ireland). Arch. Hydrobiol. 96:417–433.

SCHINDLER, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. Can. J. Fish. Aquat. Sci., 44: Suppl. 1:6–25.

SOMMER, U. 1984. Sedimentation of principal phytoplankton species in Lake Constance. J. Plank. Res. 6:1–14.

———. 1988. Growth and survival strategies of planktonic diatoms. Pp. 227–260 *in* Growth and reproductive strategies of freshwater phytoplankton, C. D. Sandgren, ed. Cambridge University Press, Cambridge.

STOERMER, E. F. 1984. Qualitative characteristics of phytoplankton assemblages. Pp. 49–67 *in* Algae as ecological indicators, L. E. Shubert, ed. Academic Press, London.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: the role of limiting nutrients. Ann. Rev. Ecol. System. 13:349–372.

TILHAM, D. R. KIESLING, R. STERNER, S. S. KILHAM, AND F. A. JOHNSON. 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. 106:473–485.

WETZEL, R. G. 1979. The role of the littoral zone and detritus in lake metabolism. Ergebn. Limnol. 13:145–161.

WHITMORE, T. C. 1991. Sedimentary diatom concentrations and accumulation rates as predictors of lake trophic state. Hydrobioloiga 214:163–169.

Diatom Assemblages of the Past 11,000 Years From the Yellowstone Lake Basin, Wyoming, U. S. A.

by

Brian R. Shero

Biology Department, Medaille College, 18 Agassiz Circle
Buffalo, New York 14214

with 2 figures and 1 table

Abstract: The Recent sediments of Yellowstone Lake, Wyoming, are dominated by a diatom assemblage of *Asterionella formosa, Aulacoseira italica, Fragilaria* spp., *Stephanodiscus minutulus*, and *Stephanodiscus yellowstonensis*. Year-round silica levels of 8 ppm and above contribute to the abundance of diatoms. Lake sediments currently being deposited are up to 90 % amorphous silica. Older lake sediments, both above and below current water level, have similarly high silica/diatom content.

The distribution of diatom species across time and space is highly variable. Sediment cores representing the past 4,000 years show an essentially modern assemblage throughout. Sediments from 5,000–11,000 years contain different assemblages, with many taxa whose autecology is poorly known. Rare or unusual taxa, such as *Melosira teres* and *Melosira undulata*, are present in large numbers at some locations.

In order to interpret the entire postglacial lake history, diatoms from many modern and fossil deposits in the lake basin have been collected. This survey of diatom distributions seeks to locate modern analogues of the fossil assemblages. The fossil and modern assemblages examined to date show little overlap.

Introduction

Yellowstone Lake (YL), in Yellowstone National Park, Wyoming, U. S. A., is a unique and poorly understood ecosystem. Silica levels of 8 ppm and higher from May to August (E. P. A. 1972) contribute to an abundance of diatoms. Lake sediments are up to 90 % amorphous silica/diatoms (Otis et al. 1977).

Previous research on YL diatoms indicated that the modern diatom assemblage has been relatively stable over at least the past 2000 years, with a possible trend toward decreased diatom production over this time (Shero 1977). This project will extend the diatom history by examining older diatom deposits from both above and below the current lake level. These diatom analyses will complement an ongoing study of lake history and lake levels

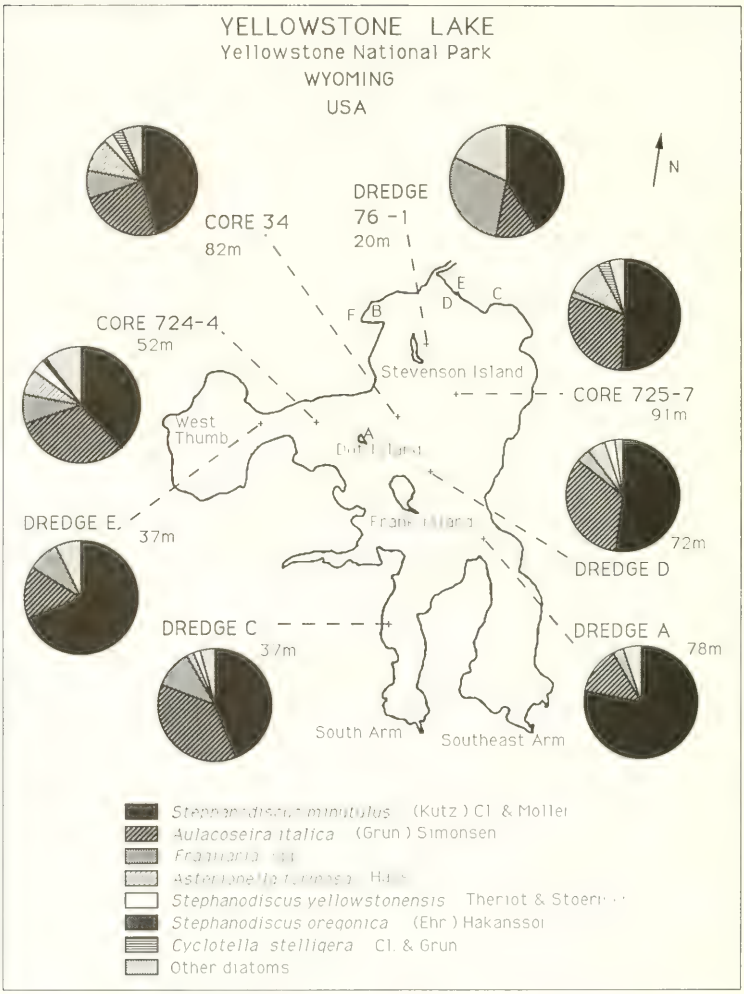


FIGURE 1. The percent abundance of the major diatom taxa in surface sediments from Yellowstone Lake, Wyoming. Letters refer to sample locations from Table 1.

being conducted by Wayne Hamilton of the National Park Service at Yellowstone National Park.

In order to interpret the postglacial history of YL, diatoms have been collected from many modern and fossil deposits in the YL basin. I have attempted to identify modern analogues of the fossil assemblages, with a long-range goal of establishing a postglacial biostratigraphy for this lake. Ecological data for the dominant taxa have been derived mainly from local conditions.

Materials and Methods

Diatomaceous material has been sampled from a variety of locations as indicated in Figure 1 and includes: exposed lake terraces, surface lake sediments collected with an Ekman Dredge, deeper lake sediments collected with gravity and piston corers, and modern diatoms collected from scrapings. Cores 23, 34, and 724-4 and 725-7 were provided by the University of Utah (Otis et al. 1977). Most of the fossil material contained frustules that needed no additional cleaning. Recent diatoms were either burned or digested in nitric acid. Diatoms were dispersed on individual coverslips and mounted in Hyrax. Identifications and counts were made under oil-immersion at 1000×.

Identifications were made using standard references (e.g., Patrick and Reimer 1966, 1975) and consultations with individual experts (mainly E. Theriot and E. Stoermer). A complete listing of taxa is found in Shero (1977). Voucher samples have been deposited in the General Collection of the Diatom Herbarium at the Academy of Natural Sciences of Philadelphia. (Mat. # 5475, ANSP G.C. slide numbers 64475–64491.) Percentage data are based on transect counts of 200–1000 frustules. Diatomite dates were estimated by W. Hamilton, NPS Geologist at Yellowstone. Core 23 dates were determined by sedimentation rates from Shuey et al. (1977).

Results and Discussion

The quantitative abundance of diatoms in Recent sediments is found in Figure 1. Qualitative abundances of diatoms in fossil and modern deposits appear in Table 1. Figure 2 indicates quantitative changes in diatom abundance in sediment Core 23 from the north-central lake basin. Data from the surface sample and those from 1,677 years and older are from Core 725-7, taken near Core 23 (see Shero 1977 for details).

Although no exact modern analogue to the fossil diatom deposits has been identified, several important conclusions can be made.

(1) The diatom assemblage of sediments 2000 years old closely resembles the diatom assemblage currently being deposited in YL sediments. The dominant taxa in modern sediments from throughout YL (Fig. 1) are similar to those of Core 23 (Fig. 2). These same taxa are common in phytoplankton samples throughout the lake. Thus, these data suggest that the lake environment has remained relatively stable over the past 2000 years. One major exception to this pattern relates to a number of *Cyclotella* species, which can comprise up to 5 % of the diatoms in Recent sediments. *Cyclotella* were almost completely absent in sediments older than 2000 years in Core 23 (Fig. 2).

(2) Older deposits (4000 + years) contain a different assemblage. *Melosira teres* is common in many of the fossil deposits (Table 1:A, B). Currently *M. teres* is found living in Sylvan Lake, a small, shallow, cold, sub-alpine lake east of YL. The fossil deposits with *M. teres* were presumably deposited under similar conditions. *Melosira teres* is not abundant in modern YL.

TABLE 1. A qualitative estimate of the most abundant diatom taxa in modern and fossil deposits in the area of Yellowstone Lake, Wyoming. Collection locations are identified in Figure 1. The most common taxa are listed under 1, with progressively less common taxa listed as 2 and 3.

A. Dot Island Diatomite – 5500 ybp; lakeshore terrace
1. *Aulacoseira italica* (Grun.) Simonsen
Melosira teres Brun.
2. *Achnanthes clevei* Grun.
Diploneis ostracodarum (Pant.) Jur.

B. Bridge Bay Cores – 4000–6000 ybp
1. *Melosira teres* Brun.
2. *Achnanthes exigua* Grun.
Aulacoseira italica (Grun.) Simonsen
Cocconeis placentula Ehrenberg
Cyclotella comta (Ehrenberg) Kütz.
Gomphonema dichotomum Kütz.

C. Mary Bay Diatomite – 5000–6000 ybp; lakeshore terrace
1. *Fragilaria vaucheriae* (Kütz.) Peters.
Melosira varians Ag.
2. *Cymbella mexicana* (Ehrenberg) Cl.
Synedra ulna (Nitz.) Ehrenberg
3. *Synedra mazamaensis* Sov.

D. Pelican Creek Delta – modern; 6 m below surface in YL
1. *Stephanodiscus minutulus* (Kütz.) Cl. and Möller
2. *Asterionella formosa* Hass.
Aulacoseira italica (Grun.) Simonsen
Diatoma tenue v. *elongatum* Lyngb.
Fragilaria construens v. *venter* (Ehrenberg) Grun.
Melosira varians Ag.
Nitzshia acicularis W. Smith

E. Pelican Creek – modern; shallow, flowing water
1. *Synedra pulchella* v. *lacerata* Hust.
2. *Fragilaria construens* v. *venter* (Ehrenberg) Grun.
3. *Cymbella cistula* (Ehrenberg) Kirchn.
Melosira varians Ag.

F. Bridge Bay Marina – modern; dock scrapings, near surface
1. *Rhopalodia gibba* (Ehrenberg) O. Müll.
Rhoicosphenia curvata (Kütz.) Grun. *ex* Rabh.
2. *Fragilaria capucina* Desm.
Fragilaria construens (Ehrenberg) Grun.
Rhopalodia gibba v. *ventricosa* (Kütz.) H. and M. Perag.
3. *Cymbella minuta* Hilse *ex* Rabh.
Epithemia turgida (Ehrenberg) Kütz.
Synedra ulna (Nitz.) Ehrenberg

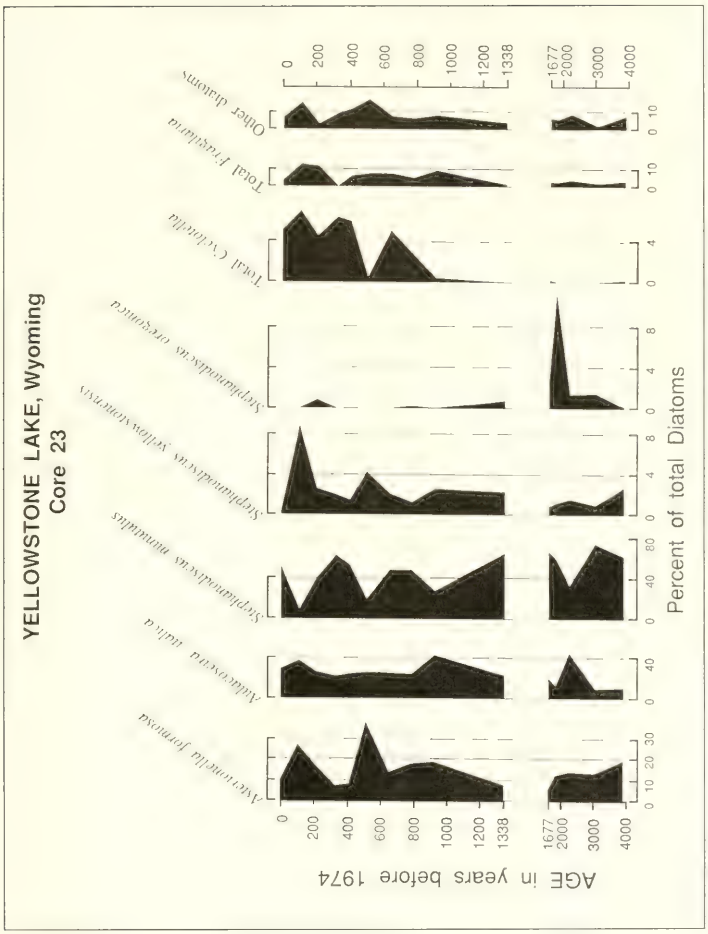


FIGURE 2. The percentage abundance of the major diatom taxa over time in Core 23 from the central basin of Yellowstone Lake, Wyoming.

(3) A diatomite at Mary Bay, estimated at 6000 ybp by W. Hamilton, is dominated by *Melosira varians* and *Fragilaria vaucheriae* (Table 1:C). Both of these taxa represent shallow water of high productivity and are found in modern YL in near-shore areas and in tributary streams. These diatomite deposits at Mary Bay are not typical of diatoms currently being deposited in the deep waters of YL.

4. The abundance of *Fragilaria* spp. (often small taxa such as *F. construens* and *F. brevistriata*) appears to be related to water depth at the time of deposition. Collections of living diatoms from a tributary stream and shallow water areas of YL contain many small *Fragilaria* (Table 1:D, E, F). The near-shore, shallow water sediments contain high percentages of *Fragilaria*, while deep water areas contain lower percentages (Fig. 1). Sherrod (1989) proposed that small *Fragilaria* were characteristic of high levels of productivity. In many cases, shallow water areas are dominated by benthonic taxa and may be more productive than deep water areas dominated by plankton. However, the controlling factor in the relative abundance of *Fragilaria* appears to be water depth, with productivity as a possible secondary factor.

5. *Stephanodiscus oregonica*, while common in the sediments throughout most of the past 2000 years (Fig. 2), is absent from nearly all surface sediment samples (Fig. 1). In addition, it has not been found alive in any of the recent plankton samples. Since this taxon accounted for nearly 10 % of the diatoms at 2000 ybp in Core 23, this is a major decline in abundance. These data support a hypothesis (Ed Theriot, personal comm.) that this taxon is characteristic of cold, pro-glacial lakes and is currently rare or absent from YL. *Stephanodiscus oregonica* is a dominant in a diatom deposit just below a layer of Glacier Peak B ash (11,200 ybp) on the north shore of YL.

6. *Stephanodiscus yellowstonensis* is currently abundant in YL and, because of its large size, it makes up a large portion of the diatom biovolume in the lake during the past 2000 years (Shero 1977; Fig. 2). This species appears to be unique to YL (Theriot and Stoermer 1984) and has replaced *S. niagarae* Ehrenberg in adjacent Alder Lake, between 8,000 and 11,000 ybp (Sherrod 1989).

7. A number of rare taxa occur in large numbers in some of the YL deposits. A surface sediment sample from 27 m in the South Arm (near Dredge C; Fig. 2) was dominated by *Melosira undulata* (Ehrenberg) Kütz., a species with many fossil occurrences in proglacial environments worldwide but few verified live occurrences. Chloroplasts have been observed in at least some *M. undulata* from YL. Another rare taxon, *Synedra mazamaensis*, is common in the Mary Bay Diatomite (Table 1:C). Both of these taxa are found in Crater Lake, Oregon (Sovereign 1958). Both Yellowstone Lake and Crater Lake occupy volcanic calderas, have high silica content, and are located at high altitude (Sovereign 1958). Sovereign also reports *M. arenaria* Moore from Crater Lake, which from my examination of modern Crater Lake sediments appears the same as *M. teres* in my YL samples.

Acknowledgements

This work was inspired and enthusiastically supported by Wayne Hamilton of the U. S. National Park Service at Yellowstone National Park, who contributed many diatom samples for analysis and provided field support for me to collect additional samples. E. Theriot and E. Stoermer have assisted the taxonomic work. Medaille College has supported my research with a Faculty Development Award. Funding for portions of the field work was provided by a grant from the UW/NPS Research Center.

Literature Cited

ENVIRONMENTAL PROTECTION AGENCY. 1972. Yellowstone National Park baseline water quality survey report. EP2.2:Y3. U. S. E. P. A., Washington, D. C. 59 pp.

OTIS, R. M., R. B. SMITH, AND R. J. WOLD. 1977. Geophysical surveys of Yellowstone Lake, Wyoming. J. Geophys. Res. 82:3705–3717.

PATRICK, R. AND C. W. REIMER. 1966. The diatoms of the United States. Vol. 1. Acad. Nat. Sci. Philadelphia, Monograph No. 13. 688 pp.

———. 1975. The diatoms of the United States. Vol. 2, Pt. 1. Acad. Nat. Sci. Philadelphia, Monograph No. 13. 213 pp.

SHERO, B. R. 1977. An interpretation of temporal and spatial variations in the abundance of diatom taxa in sediments from Yellowstone Lake, Wyoming. Ph.D. thesis. University of Wyoming, Laramie. 161 pp.

SHERROD, B. L. 1989. Paleolimnology of Alder Lake and its implications for Holocene tectonics in Yellowstone National Park, Wyoming. M.S. thesis. University of Pittsburg. 47 pp.

SHUEY, R. T., R. D. UGLAND, AND C. R. SCHMIDT. 1977. Magnetic properties and secular variation in cores from Yellowstone and Jackson lakes, Wyoming. J. Geophys. Res. 82:3739–3746.

SOVEREIGN, H. E. 1958. The diatoms of Crater Lake, Oregon. Trans. Am. Microsc. Soc. 77:96–134.

THERIOT, E. AND E. F. STOERMER. 1984. Principle component analysis of *Stephanodiscus*. Bacillaria 7:37–58.

Effects of Chemical Fixation on Flow Cytometric Properties of Diatoms

by

Clare E. Rogers

Department of Chemical Engineering,
University of Michigan, Ann Arbor, Michigan 48109-2099

and

Linda Sicko-Goad

Center for Great Lakes and Aquatic Sciences,
University of Michigan, Ann Arbor, Michigan 48109-2099

with 4 figures and 1 table

Abstract: We have utilized flow cytometry to assess the effects of fixation and storage on light scatter and autofluorescence values for three diatoms: *Thalassiosira weisflogii*, *Stephanodiscus binderanus*, and *Cyclotella meneghiniana*. We have also measured autofluorescence and DNA content changes in a culture of *C. meneghiniana* over a 24-hour period. Cultures of the diatoms were fixed in 1 % paraformaldehyde, 1 % glutaraldehyde, and .05M cacodylate buffer. Measurements of light scatter and autofluorescence were made with an EPICS C flow cytometer (Coulter Cytometry) using 200 mW of 488 nm excitation. Emissions were measured in the red and green-orange regions to assess fluorescence from chlorophyll. Measurements of fixed cells were compared to those of unfixed cells from the same culture. Cells were stored in the dark at 4° C for a period of 1 month, and measurements were taken several times over that period. Light scatter and fluorescence values were unaffected by fixation, but red fluorescence values dropped significantly during the storage period for *T. weisflogii*, and to a lesser extent, for *S. binderanus* in both fixed and unfixed samples. *Cyclotella meneghiniana* maintained its original scatter and fluorescence characteristics over the storage period. Duplicate samples taken every 2 hours from an unsynchronized, logarithmically growing culture of *C. meneghiniana* grown on a 6:8; L/D cycle at 15° C were fixed and stored as above for two weeks. Samples were then stained with the DNA-specific dye Hoechst 33342 at 5 mg/ml for 1 hour in the dark at room temperature. Two populations were identified by correlating DNA and chlorophyll content in a two-parameter histogram display: cells in one group contained six times the red fluorescence (chlorophyll) and 1.7 times the DNA content, on average, as cells in the second group. A small, but significant, drop in the number of cells with high DNA and chlorophyll content occurred between 1500 and 1900 hours (hours 5–9 of the light period), and returned to original levels by 2300 hours.

Introduction

Flow cytometry has been used by many investigators to analyze characteristics of phytoplankton populations, including relative cell size and shape, the fluorescence emissions of endogenous or exogenously added fluorochromes, and discrimination of dead cells, debris, and bacterial contamination (e.g., Olson et al. 1983; Chisholm et al. 1988; Olson et al. 1989; Robertson and Button 1989; Premazzi et al. 1989; Phinney and Cucci 1989). Many investigators do not have immediate access to a flow cytometer and must store samples for days before analysis can be performed. We have studied the effects of fixation and storage on light scatter and autofluorescence emissions of three cultured diatoms, and subsequently measured autofluorescence and DNA content changes in fixed samples taken over a 24-hour period from a culture of log phase *Cyclotella meneghiniana*.

Materials and Methods

For fixation experiments, $1–2 \times 10^6$ cells were taken from unsynchronized stock cultures of *Cyclotella meneghiniana*, *Stephanodiscus binderanus*, and *Thalassiosira weisflogii*.

Cells were pelleted by centrifugation, washed once in medium, and resuspended in either medium or a fixative solution containing 1 % paraformaldehyde, 1 % glutaraldehyde, and 0.05 M cacodylate buffer, pH 7.2. Samples were stored at 4° C in the dark. Duplicate samples were also taken every 2 hours over a 24-hour period from an unsynchronized, logarithmically growing culture of *C. meneghiniana* grown on a 16:8 L/D cycle at 15° C. Cells were fixed as above and stored for two weeks at 4° C in the dark.

For DNA staining, 5×10^5 cells were pelleted and resuspended in a 5 mg/ml solution of Hoechst 33342 (Sigma, St. Louis, MO) for 1 hour in the dark at room temperature.

For flow cytometry, all measurements were made with an EPICS C flow cytometer (Coulter Cytometry, Hialeah, FL) operated at either the blue 488 nm excitation line (200 mW) or the ultraviolet 364 nm line (50 mW) of an argon laser. Autofluorescence measurements were made in both the red (using a 630 longpass filter) and the green-orange (using the combination of a 590 dichroic mirror and 515 laser blocking filter) regions, and were collected with logarithmic amplifiers. Hoechst 33342 fluorescence (364 nm excitation) was collected linearly using a 440 bandpass filter. Forward and 90 ninety degree angle light scatter were collected logarithmically and used for gating as described in Results. Fluorescence and light scatter values for diatom samples run on different days can be directly compared because (1) identical photomultiplier tube and laser settings were used on all days, and (2) a fluorescent bead standard (Immunocheck Beads, Coulter) was used to align and calibrate the instrument to give identical fluorescence and scatter readings each day. Data was collected as either two parameter (2P) 64×64 channel or one parameter (1P) 256 channel histograms. Mean logarithmic fluorescence values were converted to mean linear values to facilitate data comparisons using the method of Muirhead et al. (1983).

Abbreviations used throughout include: BFL: linear blue fluorescence (DNA content); Chl: chlorophyll; CV: coefficient of variation; LFALS: logarithmic forward angle light scatter; LGFL: logarithmic green fluorescence; lin: linear; LOFL: logarithmic green orange fluorescence; log: logarithmic; LRFL: logarithmic red fluorescence; L90LS: logarithmic ninety degree light scatter; PE: phycoerythrin; 1P: 1 parameter; 2P: 2 parameter.

Results

An examination of the 2P log forward and log ninety-degree light scatter plots (LFALS and L90LS, respectively) collected 1 hour after fixation showed that all three cultures contained at least two distinct populations of particles (Figs. 1a, b, c). Further analysis of these populations showed that only the group with high LFALS values (designated in Figure 1 by the boxed area) contained cells with substantial red autofluorescence (LRFL) emissions. Sorting of these two populations confirmed the high LFALS group to be whole diatoms, while the lower population consisted of debris and cell fragments. Subsequent analysis was confined to the high LFALS group.

Several values derived from the flow histograms were used to assess fixation and storage effects over time: (1) the percentage of cells with "whole cell" light scatter characteristics (i.e., high LFALS and L90LS values as shown in Fig. 1), (2) the percent of these cells with high LRFL values, defined as marked for each diatom in Figures 1d, e, f (cells sorted from populations with red fluorescence values below this level were judged microscopically to be non-viable), and (3) the mean LRFL and log green-orange fluorescence (LOFL) values of these "bright" red autofluorescent cells. These values are presented in Table I.

Changes in these parameters occurred over time in two of the three tested diatom species, but appeared to be independent of fixation (Fig. 2, Table I). Neither fixation nor storage (at 4° C in the dark) had any measurable affect on the percent of cells with "whole cell" scatter characteristics; these values varied greatly between the cultures, however, with *T. weisflogii* having the lowest number of whole cells (5–8%) and *S. binderanus* having the greatest (51–57%). Variation seen in light scatter patterns between the species is probably due to their morphologic differences (Trask et al. 1982; Olson et al. 1989; Premazzi et al. 1989).

The percentage of bright red autofluorescent cells (defined as marked in Fig. 1) was not affected by fixation, but dropped over the storage period for *T. weisflogii* (from 75% to 42% for unfixed, and 78% to 51% for fixed cells), and for *S. binderanus* (77% to 60% unfixed, 76% to 60% fixed). The most dramatic drop in these values occurred in the first 24 hours of storage. *Cyclotella meneghiniana* samples were the most stable, maintaining values of 27% to 33% of cells with bright red autofluorescence.

The changes observed in mean LRFL and mean LOFL values of the bright red fluorescing cells were not significant for any of the cultures given the broad fluorescence distributions (i.e., large coefficients of variation) of the histograms. However, it is interesting to note the relative differences between diatom species in terms of these values: a comparison of mean linear fluorescence values showed *C. meneghiniana* and *T. weisflogii* to have three to five times the red chlorophyll fluorescence of *S. binderanus* (compare linear fluorescence values in Table I).

DNA content and red autofluorescence were measured simultaneously on fixed samples of *C. meneghiniana* taken over a 24-hour period and stained with the DNA-specific dye, Hoechst 33342. We have found that 364 nm excitation of chlorophyll (which occurs either directly or through energy transfer by accessory pigments), while not a peak excitation wavelength, is sufficient to produce a strong, measurable emission above 630 nm. A comparison of *C. meneghiniana* red fluorescence distributions collected with 488 nm and then 364 nm excitation, showed the percentage of red fluorescing cells and their distributions to be essentially the same (data not shown). A representative two-parameter plot of Hoechst stained cells is presented in Figure 3, along with a plot of unstained cells from the same sample. It was apparent from 1P histograms that the cells with LRFL

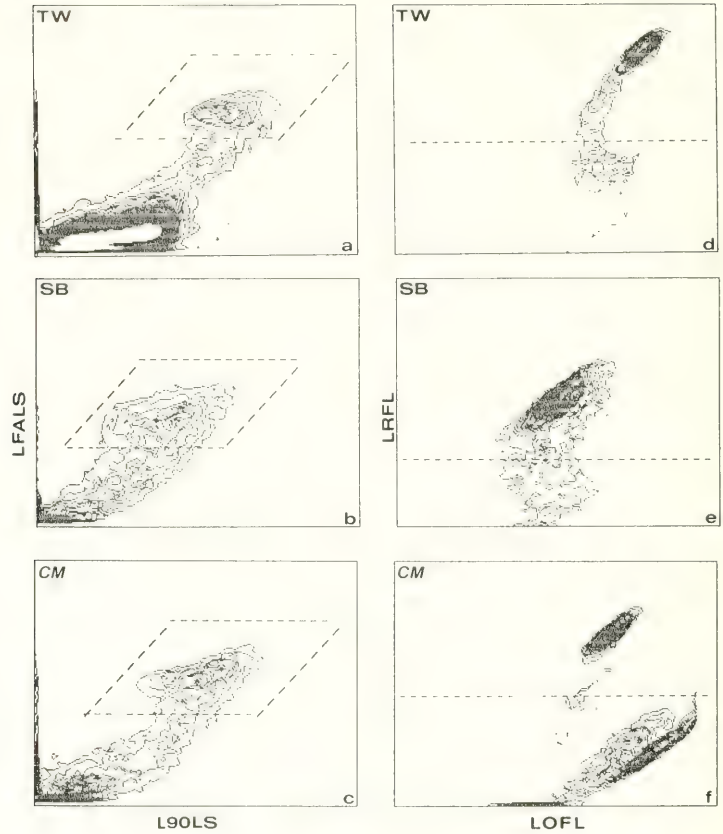


FIGURE 1. Light scatter and autofluorescence distributions for three diatoms on day 1 of fixation in 1 % paraformaldehyde and 1 % glutaraldehyde in .05 M cacodylate buffer. Cell types are: TW = *Thalassiosira weisflogii*, SB = *Stephanodiscus binderanus*, CM = *Cyclotella meneghiniana*. Figures 1a, b, c = L90LS vs. LFALS for each culture; cells sorted from the boxed area were confirmed by microscope to be whole cells. Figures 1d, e, f = LOFL vs. LRFL of this whole cell population. Cells sorted from above the line indicated on each distribution (high LRFL) were viable, while those below the line were non-viable.

values off scale negative in unstained samples increased their LRFL values upon Hoechst staining, while fluorescence emissions of cells with high LRFL values were unaffected by the stain (Fig. 3). Further analysis was confined to those cells whose LRFL values were unaffected by Hoechst staining because sorting and microscopic examination of cells

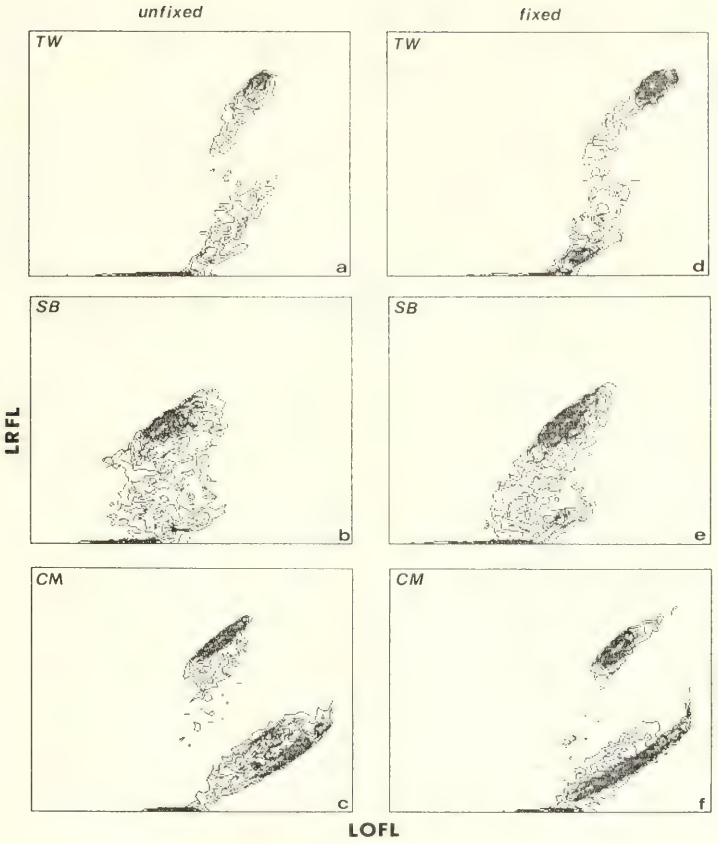


FIGURE 2. Comparison of autofluorescence distributions (LOFL vs. LRFL) for three diatoms after 28 days of storage at 4° C in the dark. Figures 2a, b, c: unfixed cells. Figures 2d, e, f: Cells fixed in 1 % paraformaldehyde and 1 % glutaraldehyde in .05 M cacodylate buffer.

with off-scale negative LRFL values showed these to be whole cells with little or no autofluorescence, and were designated as "dead" for the purposes of our analysis. We attribute the increase in LRFL emissions of these cells to secondary excitation of chlorophyll by the blue fluorescence emissions of Hoechst stain taken up non-specifically (Trask et al. 1982; Loken 1980; Premazzi et al. 1989).

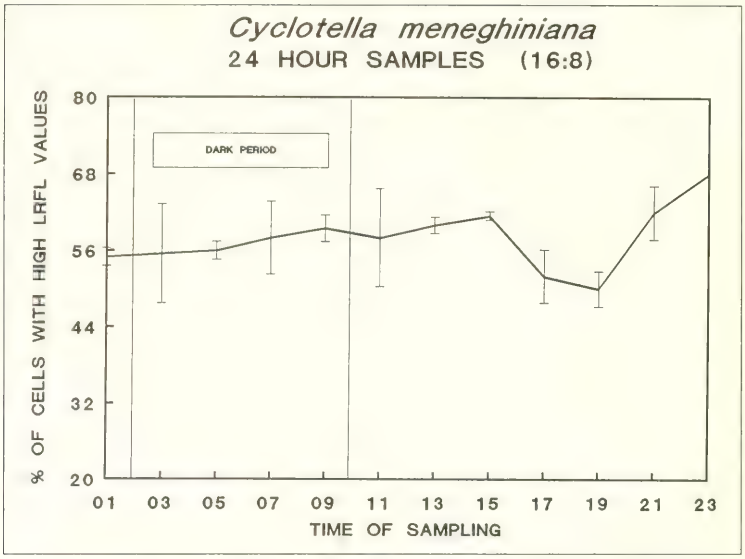


FIGURE 3. Comparison of unstained *C. meneghiniana* to cells from the same culture stained in 5 mg/mL Hoechst 33342 for 1 hour at room temperature. Figures 3a and b are 2P distributions of BFL (Hoechst 33342, DNA content) vs. LRFL (chlorophyll content) for unstained and stained cells, respectively. Figures 3c and d are 1P distributions of LRFL (chlorophyll content) resolved from the 2P distributions.

Two populations were identified by their chlorophyll and DNA contents, and the numbers of cells in each determined (see Fig. 3, boxed areas). The cells in Box 1, Fig. 3, had 6.0 times the red fluorescence and 1.7 times the Hoechst-DNA fluorescence of cells in Box 2. The percentage of cells in Box 1 was determined for each time point and plotted (Fig. 4). A small, but significant, drop in the number of cells in this population occurred between 1500 and 1900 hours (hours 5 to 9 of the light cycle), and then increased back to its original value by 2300 hours.

Discussion

These data show that storage of cultured diatoms in the dark at 4° C adversely affected the red autofluorescence emissions, but not the light scatter characteristics, of two out of three species studied. The fixation of samples prior to storage as described in Methods did not prevent this loss of fluorescence; in fact, fixation appeared to have no effect at all on the flow cytometric values determined for these samples. The loss of pigment fluorescence intensity with time in preserved samples is an important concern (Caron 1983). Since flow cytometric analysis of relative fluorescence and light scatter values is being developed as a method for identifying phytoplankton species in field samples (Yentsch and Phinney 1985; Olson et al. 1985, 1988, 1989; Li and Wood 1988), the data presented here suggest that such identification must be made cautiously if samples are stored for even 24 hours. This is because not all species will undergo changes in fluores-

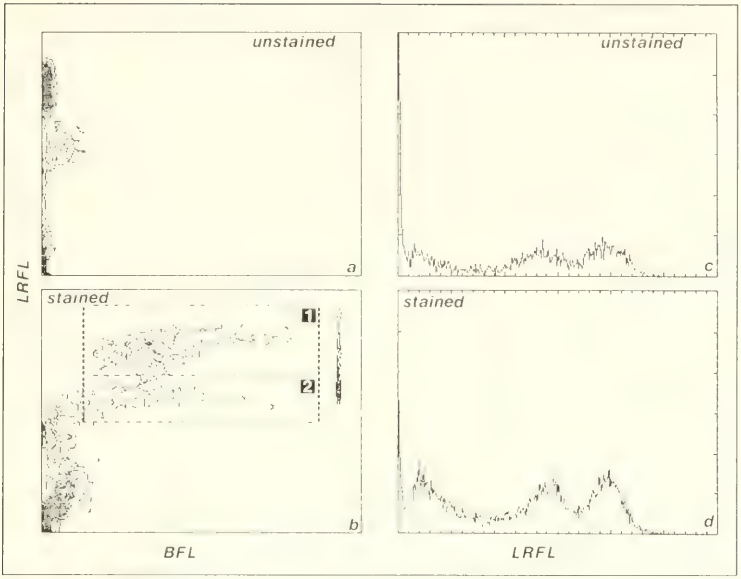


FIGURE 4. Percentage of *C. meneghiniana* cells with high red fluorescence and high DNA content versus time of day.

rescence intensity to the same extent. Our observation that *C. meneghiniana* maintained its autofluorescence intensity under the storage conditions used here simplified further analyses because we were able to store samples until flow cytometer time was available.

Our analysis of *C. meneghiniana* sampled from a logarithmically growing culture over a 24-hour period using Hoechst 33342 enabled us to correlate DNA and chlorophyll content, and to observe changes in these values as a function of time. Previous studies have indicated that DNA, protein, and chlorophyll contents fluctuate in these cultures in 24-hour cycles. Our goal is to analyze these parameters on a cell-by-cell basis using flow cytometry in order to obtain more detailed information about cell cycle events in this species. The blue fluorescence emissions of Hoechst 33342 do not overlap with the red emissions of chlorophyll (Yentsch et al. 1985; Davies and Kovacs 1990), and therefore make it an appealing choice for simultaneous analysis of DNA and chlorophyll content. For species with little or no autofluorescence in the green-orange range, fluorescein could in theory be added to allow three-color analysis of DNA, protein, and chlorophyll content.

Hoechst 33342 has been used to stain both viable and methanol fixed phytoplankton samples (Trask et al. 1982; Olson et al. 1983; Partensky et al. 1988). The fixative used in our procedures (1 % paraformaldehyde, 1 % glutaraldehyde in 0.5 M cacodylate buffer) is not comparable in effect to methanol fixation, and we observed some of the difficulties in using Hoechst that have been noted with viable samples: (1) DNA peaks with broad CVs, (2) a slight drop in LFALS readings, indicating some morphologic effects, and (3) an increase in LRFL readings for the dead cell and debris fraction. We were able to

TABLE 1. Effects of fixation on flow cytometric values of diatom species.

Cell Type[1]	Fix	Day	% in Scatter Gate[2]	% RED Autofluo-rescent[3]	LRFL (lin)[4]	LOFL (lin)[5]
TW	N	1	6	75	194 (59)	187 (48)
	N	2	5	51	189 (51)	186 (46)
	N	28	6	42	174 (32)	184 (44)
TW	Y	1	6	78	189 (51)	198 (66)
	Y	2	6	51	189 (51)	202 (74)
	Y	28	8	51	180 (39)	214(106)
SB	N	1	51	77	125 (8)	121 (7)
	N	2	51	73	122 (7)	120 (7)
	N	28	53	60	111 (5)	120 (7)
SB	Y	1	53	76	123 (7)	135 (10)
	Y	2	57	83	125 (8)	142 (13)
	Y	28	51	6	115 (6)	148 (15)
CM	N	1	36	28	175 (33)	162 (23)
	N	2	36	27	173 (32)	162 (23)
	N	28	40	33	163 (23)	157 (20)
CM	Y	1	37	28	174 (32)	179 (38)
	Y	2	32		–	–
	Y	28	31	27	167 (26)	195 (61)

[1] = Cell types: TW = *Thalassiosira weisflogii*; SB = *Stephanodiscus binderanus*; CM = *Cyclotella meneghiniana.*

[2] = Percent in Scatter Gate: Number of cells in the sample possessing "whole cell" light scatter characteristics as determined by microscope after sorting from various populations. This scatter gate is shown in Figure 1 for each cell type.

[3] = Percent Red Autofluorescent: The number of cells in the scatter gate with significant red fluorescence emissions, defined as marked in Figure 1 for each species.

[4] = LRFL (lin): Mean log red fluorescence value of the red autofluorescent population and its corresponding linear value as determined by the method of Muirhead et al. (1983).

[5] = LOFL (lin): Same as above, but for log green fluorescence values.

distinguish two separate DNA peaks despite the broad CVs and obtain valuable information without performing detailed cell cycle analysis. Further work to improve the staining of these fixed samples is needed. The increase in LRFL readings for cells with very dim fluorescence prior to staining may be due to secondary excitation of residual chlorophyll by Hoechst (Hamori et al. 1980; Premazzi et al. 1989). Previous sorting had shown these dimly red fluorescing cells to be non-viable. The fact that no changes in LRFL occurred for the viable cells indicates that energy transfer of this sort is not a significant problem in *C. meneghiniana* analysis. We will continue to explore and refine this technique in order to improve DNA peak resolution and determine optimal staining conditions.

Acknowledgments

This work has been supported by grants 88-0315 from the Air Force Office of Scientific Research and R-814194 from the Office of Exploratory Research, U. S. Environmental Protection Agency.

Literature Cited

CARON, D. A. 1983. Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. App. Env. Microbiol. 46:491–498.

CHISHOLM, S. W., R. J. OLSON, E. R. ZETTLER, R. GOERICKE, J. B. WATERBURY, AND N. A. WELSCHMEYER. 1988. A novel free-living prochlorophyte abundant in the oceanic euphotic zone. Nature 334:340–343.

DAVIES, C. DE L. AND M. KOVACS. 1990. Measurement of DNA and antigen expression of live cells using three fluorochromes and two detectors. Cytometry 11:533–538.

HAMORI, E., D. J. ARNDT-JOVIN, B. G. GRIMWADE, AND T. M. JOVIN. 1980. Selection of viable cells with known DNA content. Cytometry 1:132–135.

LI, W. K. W. AND A. M. WOOD. 1988. Vertical distribution of North Atlantic ultraphytoplankton: analysis by flow cytometry and epifluorescence microscopy. Deep Sea Res. 35:1615–1638.

LOKEN, M. R. 1980. Simultaneous quantitation of Hoechst 33342 and immunofluorescence on viable cells using a fluorescence activated cell sorter. Cytometry 1:136–142.

MUIRHEAD, K. A., T. C. SCHMITT, AND A. R. MUIRHEAD. 1983. Determination of linear fluorescence intensities from flow cytometric data accumulated with logarithmic amplifiers. Cytometry 3:251– 256.

OLSON, R. J., S. W. CHISHOLM, E. R. ZETTLER, AND E. V. ARMBRUST. 1988. Analysis of *Synechococcus* pigment types in the sea using single and dual beam flow cytometry. Deep Sea Res. 35:425–440.

OLSON, R. J., S. L. FRANKEL, S. W. CHISHOLM, AND H. M. SHAPIRO. 1983. An inexpensive flow cytometer for the analysis of fluorescence signals in phytoplankton: chlorophyll and DNA distributions. J. Exp. Mar. Biol. Ecol. 68:129–144.

OLSON R. J., D. VAULOT, AND S. W. CHISHOLM. 1985. Marine phytoplankton distributions measured using shipboard flow cytometry. Deep–Sea Res. 10:1273–1280.

OLSON, R. J., E. R. ZETTLER, AND O. K. ANDERSON. 1989. Discrimination of eukaryotic phytoplankton cell types from light scatter and autofluorescence properties measured by flow cytometry. Cytometry 10:636–643.

PARTENSKY, F., D. VAULOT, A. COUTE, AND A. SOURNIA. 1988. Morphological and nuclear analysis of the bloom-forming dinoflagellates *Gyrodinium* cf. *aureolum* and *Gymnodinium nag*. J. Phycol. 24:408–415.

PHINNEY, D. A. AND T. L. CUCCI. 1989. Flow cytometry and phytoplankton. Cytometry 10:511–521.

PREMAZZI, G., G. BUONACOURSI, AND P. ZILIO. 1989. Flow cytometry for algal studies. Water Res. 23:431–442.

ROBERTSON, B. R. AND D. K. BUTTON. 1989. Characterizing aquatic bacteria according to population, cell size, and apparent DNA content by flow cytometry. Cytometry 10:70–76.

TRASK, B.. J., G. J. VAN DEN ENGH, AND J. H. ELGERSHUIZEN. 1982. Analysis of phytoplankton by flow cytometry. Cytometry 2:258–264.

YENTSCH, C. S. AND D. A. PHINNEY. 1985. Spectral fluorescence: a taxonomic tool for studying the structure of phytoplankton populations. J. Plankton Res. 7:617–632.

Numerical Estimation of Organic Pollution Based on the Attached Diatom Assemblage In Lake Biwa and its Inflows

by

T. Watanabe

Kansai University of Foreign Studies, Kitakatahoko-cho 16-1,
Hirakata 573, Japan

and

K. Asai

Osaka Medical College, Sawaragi-cho,
Takatsuki 569, Japan

with 5 figures and 1 table

Abstract: Attached algal communities were collected from 31 sites around and 12 sites along a transect across Lake Biwa, as well as from 25 inflows into the lake, in 1988 and 1989, and DAIpo (Diatom Assemblage Index) values were generated from these collections to assess relative levels of organic pollution. There was an unexpected tendency for DAIpo values to be higher at inshore sites as compared to offshore regions, suggesting higher levels of pollution offshore. DAIpo values were commonly higher at inshore sites as compared to the inflows. Apparently pollutants from cities and villages in the north basin of the lake are carried offshore by two gyres. Higher water quality of inshore sites was due to percolating groundwater. The load of organic pollutants from each inflow was estimated using DAIpo values.

Introduction

The water pollution of lakes and streams has usually been discussed from different perspectives. In lentic water systems, water quality has been discussed from the viewpoint of the trophic system (oligotrophic-eutrophic), while in lotic waters water quality is discussed in terms of a saprobic system (oligosaprobic-polysaprobic). Water quality of lentic systems such as lakes, reservoirs, or ponds, however, are usually affected by inflows. Water quality of outflows is in fact, strongly influenced by the lentic water body as its source, or the depth of the outlet from the source. As such, many lentic waters can be considered as a single system connecting inflows and outflows.

The fundamental difference between standing and flowing waters from the perspective of water pollution makes composite discussions difficult. Accordingly, as Tsuda (1972) noted, it will be an important problem to unite the analysis of the trophic and saprobic systems. It is our opinion that a reasonable common measure to determine the degree of organic water pollution of the two ought to be developed in order to unite the two systems.

We recently developed a numerical index of organic pollution of lotic waters (Diatom Assemblage Index-DAIpo) and have subsequently investigated the application of the DAIpo index to lentic systems (Nakano et al. 1987; Watanabe and Kanechika 1988), based on the fact that the epilithic diatom assemblages in lentic and lotic waters are usually composed of common taxa. From the results of these studies, it was shown that DAIpo is useful in both lotic and lentic waters as a common index using a measure of organic water pollution (Watanabe et al. 1988c).

In the present study we collected attached algal communities from the inshore and offshore areas of Lake Biwa as well as its inflows. DAIpo values, based on diatom assemblages in the algal communities, were computed and used to compare sites relative to organic pollution.

Materials and Methods

Attached algal forms were collected from 31 sites (22 sites in the north basin, nine sites in the south basin) along the shore of Lake Biwa and from 12 sites (nine sites in the north basin, three sites in the south basin) on a transect running from C1 to C12 (Fig.1).

From among the many inflows to Lake Biwa we selected 25, all having a large flow rate, wide catchment basin, or large pollution load. Selection was based on data from the Environmental Atlas in Shiga Prefecture (Lake Biwa Research Institute 1988), Kunimatsu (1985), and the Atlas of Water Environment in Lake Biwa (The Ministry of Construction-Biwa-ko koujijimusho 1987).

At each inflow, sampling was conducted at riffles unaffected by back water from the lake.

In the north basin, surveys were made of two inflows on the northern shore, 11 on the eastern shore, and seven on the western shore. In the south basin, two inflows on the eastern shore and three on the western shore were investigated.

Sampling in the lake was conducted between June 20 and July 12, 1988, and July 20 and August 2, 1989, following the methods and protocol of Watanabe et al. (1986c, 1988c) and Watanabe and Houki (1988). Stream sampling was performed between July 20 and August 2, 1989, following the methods of Watanabe et al. (1988a).

Following collection, samples were cleaned with sulfuric acid and potassium permanganate and mounted in Caedax. Diatom taxa were identified from microphotographs at x 2000 magnification, utilizing the descriptions of Cleve-Euler (1951–1955), Hustedt (1930a, 1930b, 1959, 1961–1966) Krammer and Lange-Bertalot (1986, 1988), Lange-Bertalot and Krammer (1989), Patrick and Reimer (1966, 1975) and Watanabe et al. (1986b). The 164 taxa found in the total samples have been reported elsewhere (Watanabe and Houki 1988).

Relative abundances of the diatom taxa occurring at each site were obtained by counting the relative number of individuals present; over 600 individuals were counted in each sample.

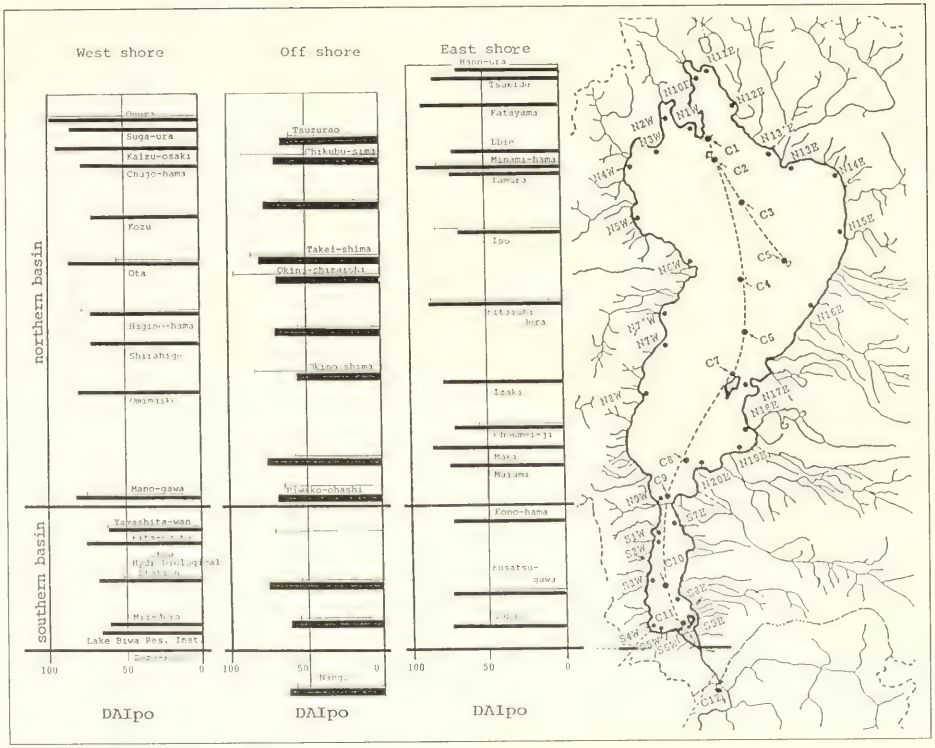


FIGURE 1. The distribution of the DAIpo values of the inshore and offshore sites. Graph bar for each site is situated opposite its respective position on the map. The bold graphs show the DAIpo values in June–July 1988. The thin graph shows the DAIpo values in July–August 1989.

DAIpo is an index based on ecological regularity, and was calculated from the following equation, which was transformed from the original equation of Watanabe et al. (1986a 1988b, 1989).

$$DAIpo = 50 + 1/2 \times (\sum_{i=1}^{m} Xi - \sum_{j=1}^{n} Yj)$$

$\sum_{i=1}^{m} Xi$: sum of relative abundance (%) of saproxenous taxa 1 to m at the sampling site.

$\sum_{i=1}^{n} Yj$: sum of relative abundance (%) of saprophilous taxa 1 to n at the sampling site.

Results and Discussion

(1) Distribution of DAIpo Values in the Lake

Distribution of DAIpo values obtained during this investigation are shown in Figure 1. In this figure, the left graphs show the DAIpo values at the west shore site, the middle graphs those of offshore sites, and the right graphs those of east shore sites. Bar graphs for each site are situated opposite their respective positions on the map. The thin graphs show the DAIpo values for 1989, bold graphs those for 1988.

This figure illustrates several features:

1. In both surveys, DAIpo values of offshore sites were less than those on inshore sites.

2. At all offshore sites, excepting island sites, and in many inshore sites, DAIpo values in 1989 were less than those in 1988.

3. At island sites, the DAIpo values in 1989 were higher than those in 1988, e.g., Chikubu-shima Island–32 points higher, Takeishima island–5 points higher, and Okino-shima is-land–29 points higher.

The first result described above seems explicable in terms of pollutants flowing into the north basin from cities, villages, and rivers being carried offshore by water currents from two gyres and resulting in a decrease in the water quality offshore. By comparison, inshore sites of this basin were of high water quality, possibly due to the inflow of percolating underground water and clean streams.

The second result may be a consequence of annual differences in precipitation during the one or two months before sampling.

At island sites in 1988, strong winds prevented us going ashore, and samples were therefore collected from the surface of buoys or anchoring ropes. In 1989, however, samples were collected directly from the vertical surfaces of rocky shoreline. Accordingly, the third result may be related to differences in the substrate on which the algal communities were attached. Watanabe and Suzuki (1989), however, confirmed that diatom assemblages were not affected by substrate differences, and therefore the higher DAIpo values of island sites in 1989 may be caused by a "self-purification" by the dense and abundant algal community attached to the surface of the rocky shoreline of the island.

If this interpretation is correct, the same phenomenon should also be evident from rocks at lake shore sites. As shown in Figure 1, the DAIpo values of rocky sampling sites in

the north basin, N1W-N3W, N10E, N12E, N19E in 1988 and N2W, N15E, N16E in 1989 were very high (83–100). Further studies are necessary, however, before any firm conclusion can be drawn concerning this phenomenon.

(2) DAIPO OF INFLOWS

The DAIpo values of each inflow are shown in Table 1. Strong correlations are observed between the DAIpo values of inflows and the average value of the year in COD, T-P and T-N, as shown in Figure 2. This supports our contention that the DAIpo values can be used as an observable quantity in the same manner as values derived from chemical analyses.

In this study, the catchment basin of this lake was divided into eight areas in the north basin and two areas in the south basin. It can be considered that the load of pollutants through the inflows in each area is near the total of loads of selected inflows of each respective area. The average degree of water pollution of inflows in each area can be then obtained by the following equation.

$$P = (DAIpo \times F) / B$$

P: the average of DAIpo values of inflows in each area.

B: total flow rates of inflows from 1 to n.

(DAIpo × F): sum of the DAIpo values times flow rate of the inflow from 1 to n.

The P value in each area is shown in Table 1 and Figure 3. At the western shore of the north basin, the P value decreased in serial order from the northern area (NWI) to the southern area (NWIII). The P values at the eastern shore were less than those at the western area, probably due to the load of sewage and waste water from several cities and surrounding areas.

In the south basin, the P values in both eastern and western areas (SE, SW) were remarkably less.

(3) THE DAIPO VALUES OF INSHORE SITES AND THE P VALUE

It is assumed that the water quality of inshore sites in each area is closely related to the P value of its area. With this assumption, we compared the P value with the average of DAIpo values of all inshore sites in each area.

The DAIpo values of 25 inflows are represented graphically in Figure 3. In the rectangular frame in this figure, the bold graph bar shows the P value, and the thin graph bar the average of DAIpo values of all inshore sites in each area. As Figure 3 shows, in both the north and south basins, P values of the eastern area are less than those of the western area. Taken together with the results shown in Figure 4, this appears as strong evidence that pollutional loads through inflows in the eastern area are an important source promoting eutrophication of the lake.

The average DAIpo values of all inshore sites exceeded the P values in all areas except NWI and NWII. In recent papers, Watanabe et al. (1989) and Watanabe and Kanechik (1986) reported that the water quality of reservoirs fed by clean stream water inflows is generally lower than that of the stream itself. The present result contradicts that conclusion due to the inflow of percolating underground water. Conversely, the average of DAIpo values (73) at offshore sites of the north basin in 1989 was less than those of the P value (76) of 25 inflows surveyed in 1989 in the north basin. If we take the DAIpo values in

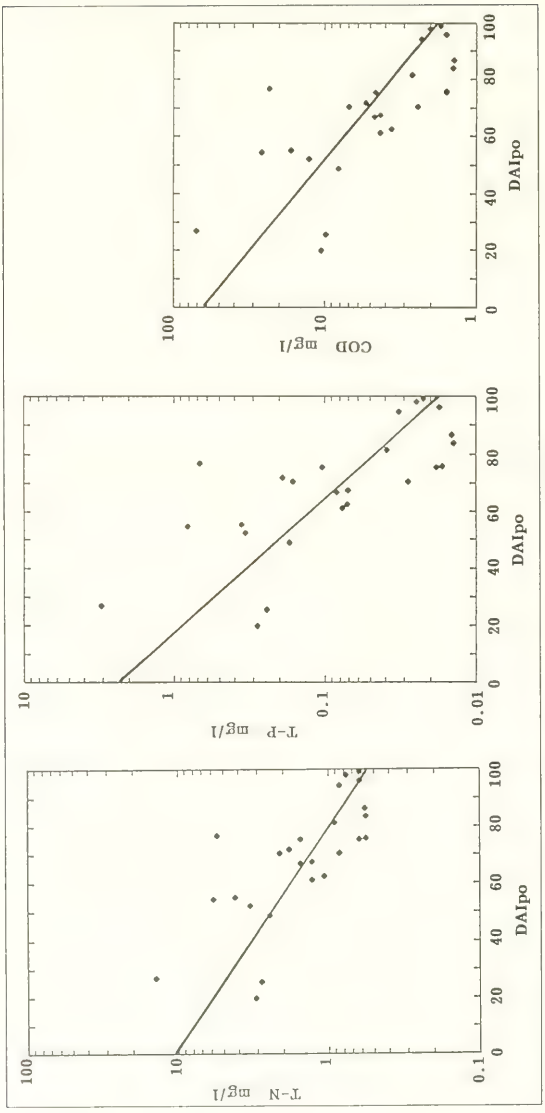


FIGURE 2. The correlations between the DAIpo values of 25 inflows and the average value of the year in T–N, T–P, and COD. T–N: r = -0.7353, T–P: r = -0.7372, COD: r = -0.7360.

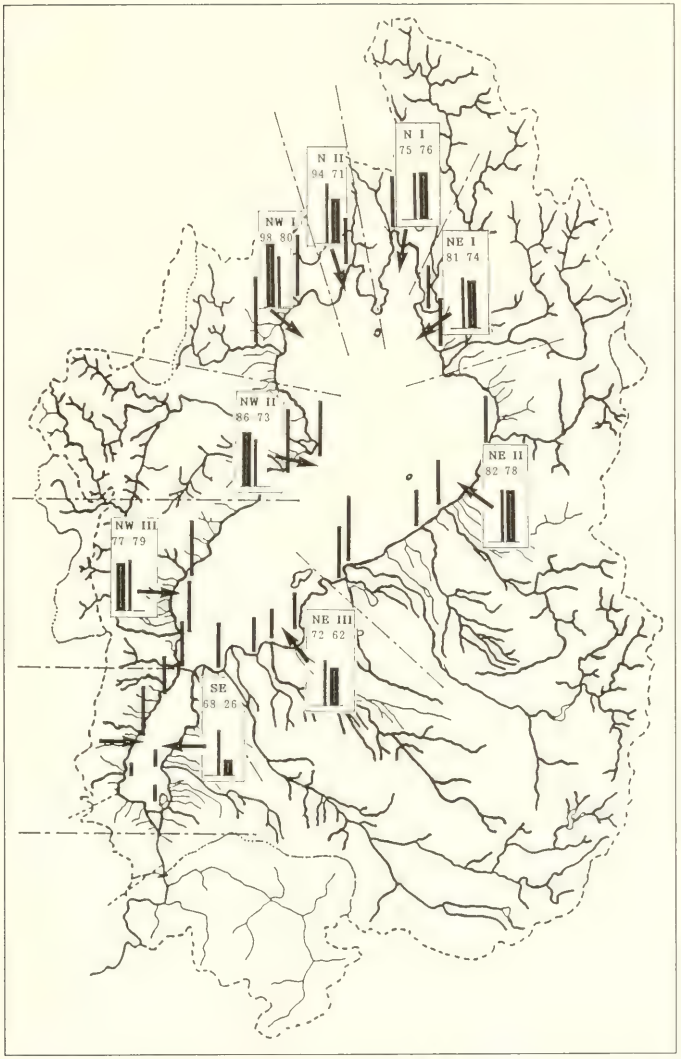


FIGURE 3. Comparison of the P value (bold graph) with the average DAIpo values of all inshore sites (thin graph) in each area (in the rectangular frame). The outside graph bar from the frame shows the DAIpo value of each inflow.

offshore sites as being representative values of water quality in the north basin, our observed results agree with those reported by Watanabe et al. (1989).

In the south basin, the average DAIpo values at offshore sites was 59, much higher that the P value (39) of five inflows. In this basin, flow rates of inflows totaled 0.0001, however, and water from the northern basin had a DAIpo value of 63.

Considering these facts, although eutrophication of the south basin should have occurred as a consequence of the load of pollutants from inflows, a large quantity of inflow from the north basin contributed greatly towards avoiding strong eutrophication.

(4) Pollutional Load From Inflow and Water Quality at Lake Shore Sites

Organic pollution load of each inflow was calculated from the following equation.

$$L = (100 - DAIpo) \times F$$

L: organic pollution load based on the DAIpo value (DAIpo load).

F: low rate (ton.Y^{-1}).

The L value of each inflow is shown in Table 1. Organic pollution load from inflows, the location of cities and towns, and the situation of the gyres are shown in Figure 4.

The area containing lake shore sites with DAIpo values over 75 is shown by the oblique line in Figure 4.

In the northeast area of the north basin, the pollution load from the River Yogo, the River Ane, the River Amano, the River Inukami and the River Uso was large, as shown in Figure 4. The pollution loads from these rivers are the major source of eutrophication in the north basin. In this area, lake water near the shore may be affected by sewage and waste water from the cities of Nagahama and Hikone and their vicinities. DAIpo values at inshore sites in this area, however, were only slightly larger than those of inflows, as shown in Figure 3. This phenomenon is inexplicable unless we assume water purification by the eruption of ground water at the lake shore.

The pollution load of the River Ado flowing along the northwestern shore is also large, and the DAIpo value at N6W site near the mouth of this river was very high in 1988. However, in 1989 it was very low. This was due to the annual fluctuation of the eruption of groundwater.

In a former investigation (Watanabe et al. 1990), we estimated that pollutants flowing into the north basin from cities and villages and carried offshore by water currents from the gyres decrease water quality of offshore sites. In the present research, however, it was assumed that the pollution loads from inflows would also be closely related to the worsening of offshore water quality.

Kobayashi (1990) confirmed that the seepage flow rate at a site near the mouth of the River Yasu the highest (110 l m^{-2} day^{-1}) and that of the River Hino the second highest, (91 l m^{-2} day^{-1}) at the east shore of this lake.

From these observations, high water qualities at shore sites in this area, which occur irrespective of the high pollutional loads from the rivers, seem due to a high seepage flow rate. Furthermore, the two rivers enter the lake near the narrow section connecting the north and south basins, far away from the gyre in the north basin. As a result, the effect of the pollutional loads from the two inflows on the eutrophication of the south basin will be much greater than that of the north basin.

TABLE 1. The DAIpo value, flow rate, and pollutional load of each inflow in 10 catchment areas and the average of DAIpo values of inflows in each area (P value).

		Name of river		DAIpo	Flow (ton/y)	Pollutional load (DAIpo load)	DAIpo x flow	Total (A)	Total of flow (B)	$\overline{M}$ of DAIpo (A/B)
Northern basin	Northern bay	NI								
		R. Oo	RNW12:	75.92:	3268:	78696:	–	–	–	75.9 (76)
		NII								
		R. Ooura	RNW13:	70.61:	4014:	117987:	–	–	–	70.6 (71)
	Eastern shore	NE I								
		R Yogo	RNE1	62.57	10604	396910	663492.28			
		R. Ane	RNE2 :	75.69:	60669:	1474790:	4592036.61	5255528.89	71273	73.7 (74)
		NE II								
		R. Amano	RNE3	67.05	11617	382731	778919.85			
		R. Inukami	RNE4 :	71.99:	11095:	310748:	798729.05			
		R. Uso	RNE5	52.29	8233	392803	430503.57	4720112.60	60244	78.4 (78)
		R. Echi	RNE6	94.77	216194	136902	2482405.38			
		R. Daido	RNE7 :	73.95:	3105:	80892:	229614.75			
		NE III								
		R Choumeji	RNE8	55.16	6431	288346	354733.96			
		R. Hino	RNE9 :	48.78:	17946:	919262:	875405.88	3978098.01	63762	62.4 (62)
		R. Kato	RNE10 :	54.50:	2462:	112013:	134179.00			
		R Yasu	RNE11	70.79	36923	1078700	2613779.17			
	Western shore	NW I								
		R. Chinai	RNW14:	96.44:	8112:	28898:	782321.28	1625705.49	16613	97.9 (98)
		R. Ishida	RNW15:	99.21:	8501:	6723:	843384.21			
		NW II								
		R. Ado	RNW16:	84.07:	49441:	787663:	4156504.87	4751106.38	55488	85.6 (86)
		R. Kamo	RNW17:	98.33:	6047:	10078:	594601.51			
		NW III								
		R. Ootani	RNW18	86.57	1002	13454	86743.14			
		R. Wani	RNW19:	81.58:	1959:	36087:	159815.22	390018.81	5076	76.8 (77)
		R. Mano	RNW20:	67.83:	2115:	68044:	143460.45			
Southern basin	Eastern shore	SE								
		R Kusatsu	RSE1 :	25.80:	2482:	184177:	64035.60	75845.90	2927	25.9 (26)
		R Ookami	RSE2 :	26.54:	445:	32688:	11810.30			
	Western shore	SW								
		R. Tenzin	RSW3 :	61.26:	990:	38349:	60647.40			
		R. Oomiya	RSW4 :	75.81:	596:	14415:	45182.76	112012.84	1897	59.1 (59)
		R. Yana	RSW5 :	19.88:	311:	24916:	6182.68			

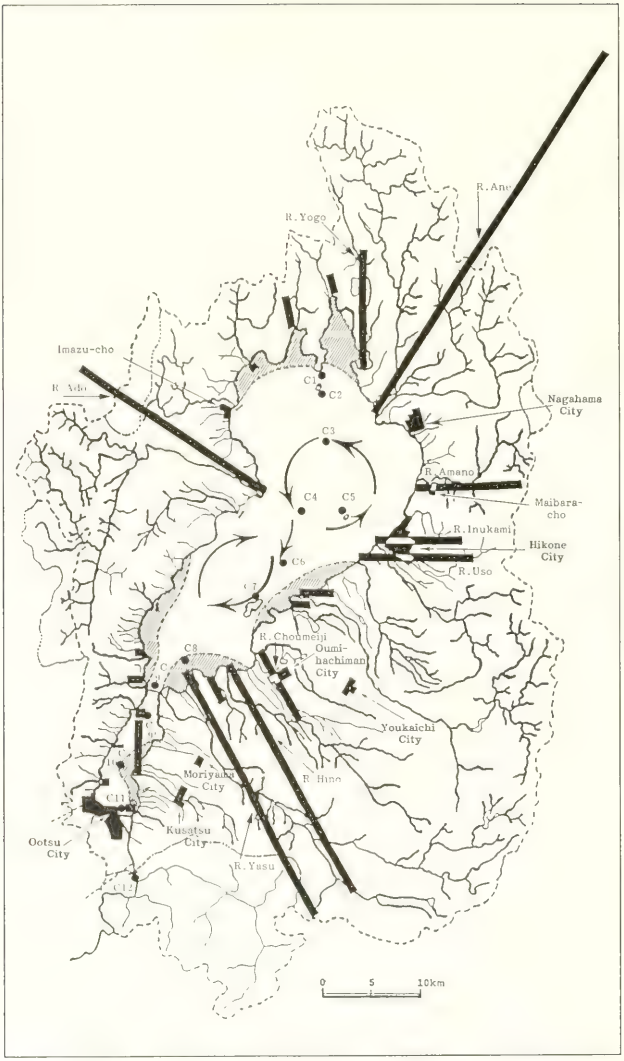


FIGURE 4. Organic pollutional loads from inflows (bold graph), the cities and towns, and the situation of the gyres. Clean water areas with inshore sites of DAIpo values exceeding 75 shown by the oblique line.

(5) The Area of Inshore SItes HAving Large Daipo Value and Eruption of Groundwater

As shown in Figure 4, the north basin has five clean water areas with DAIpo values exceeding 75, and one such area in the south basin. These areas were included within the clean water areas revealed through a survey in 1988 (Watanabe et al. 1990). In the north basin, four areas agree well with those having a large volume of eruption of groundwater in the distributional map of seepage flow rate (Kobayashi 1990: Fig. 5). That is, the largest seepage flow rates in the lake occur at the northern two areas and southern area along the western shore in the north basin, and near the mouths of the rivers Hino and Yasu at the eastern lake shore.

In the south basin, many sites having high DAIpo values are present at the eastern area, however, the River Kusatsu, with a large pollution load, flows into the area (Fig. 4). Based on the study of the epilithic diatom flora, Higo and Watanabe (1978) have assumed the eruption of groundwater at the eastern bottom, and Kobayashi (1990) has reported the mean seepage flow rate in the eastern area to be 16 times that of the western area in the south basin.

From these facts we may conclude that the effect of eruption of groundwater greatly influenced water quality at inshore sites in the eastern area.

Seepage flow rate at the eastern shore of Okino Island, however, is relatively small. At sites in this area and at four island sites, Chikubu Island, Okinoshiraishi Island, Takei Island, and Okino Island, high DAIpo values cannot be explained in terms of a large seepage flow rate of groundwater. All the above-mentioned sites were surrounded by rocky shores, and the algal community growing on the rocks extended over a wide area. Higher water qualities observed in this area may be attributed to a "self-purification" of a large quantity of the attached algal community.

Summary

Attached algal communities were collected from the inshore and offshore sites of Lake Biwa and its inflows, and DAIpo values were computed for each site from the species composition of the diatom assemblage in the algal community.

Results may be summarized as follows:

(1) In both 1988 and 1989, DAIpo values of offshore sites were lower than those of inshore sites. Lower water quality of offshore sites seems to be due to pollutants flowing into the north basin from cities, villages, and rivers, and then carried offshore by water currents from two gyres. Conversely, water quality of inshore sites of this basin were very high, probably resulting from the inflow of percolating underground water and clean streams.

(2) In both offshore areas, except island sites, and at many inshore sites, DAIpo values in 1989 were lower than those in 1988. Annual differences in precipitation during the one or two months before the sampling time may have caused the difference.

(3) The catchment basin of this lake was divided in eight areas in the north basin and two areas in the south basin. For each area, the average DAIpo values of inflows in each area (P value) were calculated. In both the north and south basins, P values of the eastern area were less than those of the western area. This strongly indicates that pollution loads through inflows in the eastern area were an important source promoting eutrophication of Lake Biwa.

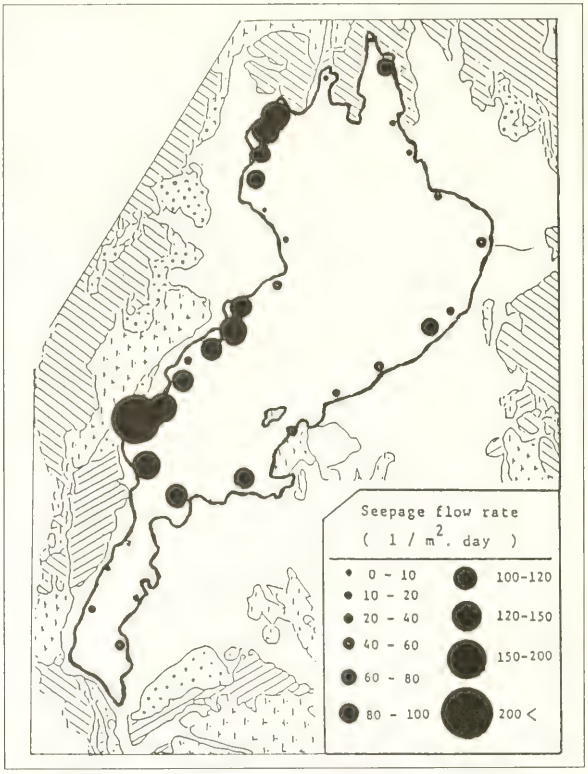


FIGURE 5. The distribution map of seepage flow rate of the underground water in Lake Biwa. (M. Kobayashi 1990).

(4) Considering the DAIpo value of water flowing from the north basin to the south basin and the P value of five inflows in the south basin, a large quantity of water flowing from the north basin may greatly reduce eutrophication of lake water in the south basin.

(5) This study clearly showed there to be five inshore areas with large DAIpo values in the north basin, and one in the south basin. These areas are included within the clean water areas revealed through the study in 1988 (Watanabe et al. 1990). Five of the inshore areas coincide with having a large volume of eruption of groundwater.

(6) The DAIpo values of the inshore sites surrounded by rocky shore and island sites were very high, as a result of a "self- purification" of a large quantity of the attached algal community

Acknowledgements

This work is a part of the research sponsored by the Lake Biwa Research Institute. And we are indebted to Takuo Nakajima for providing the data of water chemistry variables and Machiko Nishino, Mrs. Akiko Houki, and Michiaki Sumita who extended us their kind assistance.

Literature Cited

CLEVE-EULER, A. 1951. Die Diatomeen von Schweden und Finnland. Pt. 1. K. Svenska Vetenskapsakad. Handl. 2:1–163.

———. 1952. Die Diatomeen von Schewden und Finnland. Pt. 5. K. Svenska Vetenskapsakad. Handl. 3:1–153.

———. 1953a. Die Diatomeen von Schweden und Finnland. Pt. 2. K. Svenska Vetenskapsakad. Handl. 4:1–158.

———. 1953b. Die Diatomeen von Schweden und Finnland. Pt. 3. K. Svenska Vetenskapsakad. Handl. 4:1–255.

———. 1955. Die Diatomeen von Schweden und Finnland. Pt. 4. K. Svenska Vetenskapsakad. Handl. 4:1–232.

HIGO, M. AND T. WATANABE. 1978. Biological classification of the water mass in the southern basin of Lake Biwa, using the similarity index on pelagic diatom communities. Jpn. J. Limnol. 39:130–136.

HUSTEDT, F. 1930. Bacillariophyta (Diatomae). Die Susswasser- Flora Mitteleuropas, Heft 10, A. Pascher, ed. 466 pp. Gustav Fischer, Jena.

HUSTEDT, F. 1927–1930. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. Vol. 7, Pt. 1 *in* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, L. Rabenhorst, ed. Akademische Verlagsgesellschaft. 920 pp.

———. 1931–1959. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. Vol. 7, Pt. 2 *in* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, L. Rabenhorst, ed. Akademische Verlagsgesellschaft. 845 pp.

———. 1961–1966. Die Kieselaglen Deutschlands, Österriechs und der Scweiz. Vol. 7, Pt. 3 *in* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, L. Rabenhorst, ed. Akademische Verlagsgesellschaft. 816 pp.

KOBAYASHI, M. 1990. Distribution of seepage flow rate in Lake Biwa. Pp. 38–59 *in* the 8th symposium report on the study of Lake Biwa. Lake Biwa Res. Inst.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae. Naviculaceae. Band 2, Pt. 1 *in* Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds. Gustav Fischer Jena. 876 pp.

———. 1988. Bacillariophyceae. Bacillariaceae, Epithemiaceae, Surirellaceae. Band 2, Pt. 2 *in* Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig, and D. Mollenhauer, eds. Gustav Fisher, Jena. 596 pp.

KUNIMATSU, T. 1985. Kasen suishitsu no suishitsuodakushihyo niyoru hyogen. Lake Biwa Res. Inst. Bull. 3:68–72.

LAKE BIWA RESEARCH INSTITUTE. 1988. Shiga prefecture regional environmental atlas, land use and water budget by river basins (1–3).

LANGE-BERTALOT, H. AND K. KRAMMER. 1989. *Achnanthes*, eine Monographie der Gattung. Bibl. Diatomologica 18:1–393.

NAKANO, K., T. WATANABE, N. USAMAN, AND A. SYAHBUDDIN. 1987. A fundamental study of overall conservation of terrestrial and freshwater ecosystems in a mountain region of Western Sumatra: Vegetation, Land-use and Water quality. Mem. Kagoshima Univ. Res. Center S. Pacific. 8:87–124.

PATRICK, R. AND C. W. REIMER. 1966. The Diatoms of the United States, Exclusive of Alaska and Hawaii, Vol. 1. Acad. Nat. Sci. Philadelphia, Monograph No. 13, 688 pp.

———. 1975. The Diatoms of the United States, Part 2, Acad. Nat. Sci. Philadelphia, Monograph No. 13, 213.pp.

THE MINISTRY OF CONSTRUCTION-BIWA-KO-KOUJIJIMUSHO. 1987. Water environment atlas of Lake Biwa. 125 pp.

TSUDA, M. 1972. Ecology of water pollution. Kogai-Taisaku-Gijutsu-Doyukai Co., Ltd. Tokyo. 240 pp.

WATANABE, T. AND A. HOUKI. 1988. Attached diatoms in Lake Biwa. Jpn. J. Diatomol. 4:21–48.

WATANABE, T. AND M. KANECHIKA. 1986. Application of DAIpo (Diatom Assemblage Index to organic water pollution) to lentic environment. Jpn. J. Diatomol. 2:153–162.

WATANABE, T., K. ASAI, AND A. HOUKI. 1985. Epilithic diatom assemblage to organic water pollution (DAIpo) and its ecological significance. Annual Report of Graduate Division of Human Culture, Doctoral Degree Program, Nara Women's University, ed. and pub. 1:76–94.

———. 1986a. Numerical estimation to organic pollution of flowing water by using the epilithic diatom assemblage-Diatom Assemblage Index (PAIpo). The Science of the Total Environment 55:209–218.

WATANABE, T., K. ASAI, A. HOUKI, S. TANAKA, AND T. HIZUKA. 1986b. Saprophilous and eurysaprobic diatom taxa to organic pollution and diatom assemblage index (PAIpo). Jpn. J. Diatomol. 2:23–73.

WATANABE, T., K. NEGORO, G. FUKUSHIMA, H. KOBAYASI, K. ASAI, T. GOTOH, T. NAGUMO, T. KOBAYASHI, S. MAYAMA, AND A. HOUKI. 1986c. Studies on the quantitative water quality estimation on freshwater pollution using diatom communities as the biological indicator. Research Project in Review 1986, Nissan Science Foundation. 139–167.

WATANABE, T., K. ASAI, AND A. HOUKI. 1988a. Numerical water quality monitoring of organic pollution using diatom assemblages. Pp. 123–141 *in* Proceedings of the 9th International Diatom Symposium, F. E. Round, ed. BioPress Ltd and Koeltz Scientific Books, Bristol and Koenigstein.

———. 1988b. Biological information closely related to the numerical index DAIpo (Diatom Assemblage Index to Organic Water Pollution). Jpn. J. Diatomol. 4:49–58.

WATANABE, T., T. YAMADA, AND K. ASAI. 1988c. Application of diatom assemblage index to organic water pollution—DAIpo—to standing waters. Jpn. J. Wat. Poll. Res. 11:765–773.

WATANABE, T. AND N. SUZUKI. 1989. Effect of substrata on flora of attached diatom assemblage with reference to biological water quality assessment. Jpn. J. Limnol. 50:129–137.

WATANABE, T., K. ASAI, AND T. YAMADA. 1989. The change of organic pollution degree of lotic waters according by construction of the dammed lake. *In* Symposium report on effects of artificial modification of the river environment of living organisms. Jpn. J. Limnol. 50:69–70.

WATANABE, T., K. ASAI, A. HOUKI, AND M. SUMITA. 1990. Numerical simulation of organic pollution based on the attached diatom assemblage in Lake Biwa (1). Jpn. J. Diatomol. 5:9–20.

Seasonal Change of Diatoms in the Plankton of the Vistula River Above and Below the Goczalkowice Reservoir, Poland

by

K. T. Kiss

Hungarian Danube Research Station, Hungarian Academy of Sciences,
H-2131 Göd, Jávorka S. u. 14, Hungary

and

G. Pajak

Inst. Freshwater Biol. Hydrobiol. Sta., Polish Academy of Sciences,
P-43230 Goczalkowice, ul. Jeziorna 82, Poland

with 4 figures, 1 table, and 2 plates

Abstract: Phytoplankton of the River Vistula was studied monthly upstream and downstream from the Goczalkowice Reservoir (southern Poland) in 1982–1983. A total of 290 phytoplankton taxa were identified, of which 138 were diatoms. Number of taxa differed between the two sampling points, with 78 pennate taxa and 19 centric taxa identified at Drogomysl (upstream from the reservoir) and 95 pennate and 24 centric taxa found at Goczalkowice (downstream from the reservoir).

Flooding exerted a considerable influence on the composition of the diatom taxa in the phytoplankton upstream from the reservoir. During flood events, the number of periphytic diatom cells in the plankton increased. *Achnanthes minutissima*, *Cymbella silesiaca*, *Navicula gregaria*, and *N. lanceolata* were abundant in spring collections. On the other hand, euplanktonic species became dominant during low water periods.

The Goczalkowice Reservoir has a fundamental effect on the phytoplankton of the river. Downstream from the reservoir the phytoplankton community is similar in many respects to longer, eutrophicated rivers of Central Europe where centric diatoms predominate. In spring the most characteristic species at the downstream site were *Cyclotella comta*, *Stephanodiscus invistitatus*, and *S. minutulus*, while in summer and autumn these species were joined by *C. pseudostelligera*. Pennate taxa that were frequent at this site included euplanktonic forms such as *Asterionella formosa*, *Nitzschia fruticosa*, *N. palea*, and *Fragilaria ulna* v. *acus*.

On the basis of morphological investigations we consider *Stephanodiscus rugosus* and *Pseudostephanodiscus perforatus* to be synonyms of *S. minutulus*.

From a hydrobiological point of view, the Goczalkowice Reservoir forms a boundary between the upper and middle sections of the River Vistula.

Introduction

The first detailed description of the phytoseston of the River Vistula, written by Starmach (1938), contains an extensive analysis of diatoms. This initial paper was followed by many others that summarized the results of investigations in different areas, from the Biala Wiselka area to around Tczew (Cabejszek et al. 1959; Hanak-Schmager 1974; Klimowicz 1981; Kwadrans 1986; Kyselowa and Kysela 1966; Turoboysky 1962; Tyszka-Maczkiewicz 1983; Uherkovich 1970; Wysocka 1950). Several hydrobiological studies of the Goczalkowice stretch of the Vistula have been undertaken in the past few decades. These studies have concentrated on long-term phytoplankton changes within the reservoir. Little attention was paid to the algal communities flowing into the reservoir from upstream.

The results of a one-year study on the qualitative and quantitative aspects of diatom phytoplankton communities in the Vistula River in the vicinity of the Goczalkowice Reservoir form the basis of the present report. Observations on other algal groups can be found in Pajak and Kiss (1990).

Materials and Methods

Description of the Study Area

The Goczalkowice Reservoir was constructed between 1950–55, for water retention and supply purposes. The major source of the reservoir is the River Vistula, which provides 80 % of its water (Fig. 1). Before reaching the reservoir the River Vistula has features of a mountainous river, including a swift current and a stony-gravel bottom. The reservoir is also fed by a small tributary, the River Bajerka.

The upper reach of the Vistula in the mountains is only 5 % of its total length. The Wisla-Czarne Reservoir is located in the mountains where the Biala and Czarna Wiselka rivers meet, and it has a retention time of 1–2 months. Approximately 15–20 km downstream from this reservoir, the angle of slope of the river decreases (to 0.6 %). The river then flows into the Goczalkowice Reservoir 55 km downstream. Goczalkowice Reservoir is limnic with large, shallow areas. Its drainage basin is 532 km^2 and the retention time is 3–6 months. At maximum water level the reservoir has an area of 3200 ha and a volume of 168 million m^3. Maximum length of the reservoir is 12 km, maximum width is 6 km. Mean depth of the reservoir is 5.2 m and discharge ranges from 0.45 m^3s^{-1} to 240 m^3s^{-1}.

Sample Collecting and Processing

Samples were taken monthly, November 1982–October 1983, at two stations. One station was situated on the Vistula, 3 km upstream from the inflow to the reservoir, near the village of Drogomysl. At this locality the river had swift current and a stony-gravel bed. The second station was 1 km downstream from the dam at Goczalkowice, and here the river bed consisted of stones.

Samples were collected with two-liter containers from a depth of approximately 20 cm in the middle of the river. Samples were fixed in Lugol's solution. Quantitative analysis was performed using Utermohl's method (Lund et al. 1958). Sedimented samples weredigested by H_2O_2, washed in distilled water, and mounted in Pleurax resin. Small

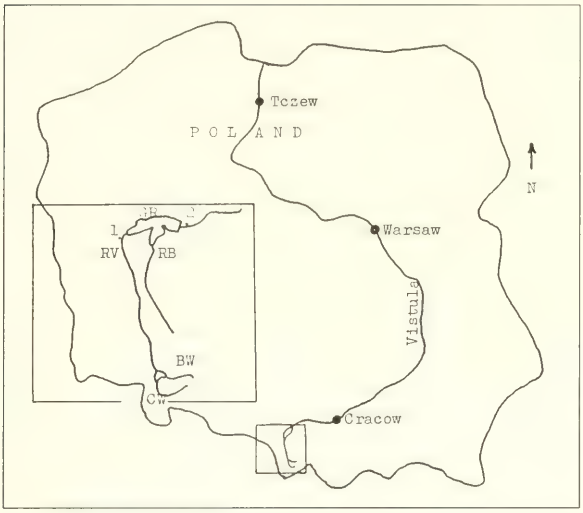


FIGURE 1. Sketch map of the study area: 1, sampling point at Drogomysl; 2, at Goczalkowice; GR, Goczalkowice Reservoir; RV, River Vistula; RB, River Bajerka; BW, River Biala Wiselka; CW, River Czarna Wiselka.

diatoms were identified with the aid of electron microscopy (TEM-a Tesla BS 500; SEM-a JEOL JSM-35). Percent composition of the Thalassiosiraceaen species was determined with TEM (Kiss 1986).

The constancy (C) of a species was calculated as C = N/S *100, where N = number of samples in which the species was present, and S = total number of samples. A species was given a constancy value 5 if C = 80–100 %, 4 if C = 60–80 %, etc.

Results

A total of 290 algal taxa have been found in the Goczalkowice stretch of the Vistula. Of these, 18 belong to the Cyanophyta, 9 to Euglenophyta, 12 to Chrysophyceae, 2 to Xanthophyceae, 6 to Cryptophyceae, 3 to Dinophyceae, 97 to Cholorophyceae, and 5 to Conjugatophyceae (Pajak and Kiss 1990). A total of 138 diatom taxa were recorded, including 27 centric and 111 pennate taxa. The presence and constancy values of diatoms and their abundance in four representative samples are shown in Table 1.

Large qualitative differences exist in the planktonic diatoms of the Vistula between stations upstream and downstream from the Reservoir (Fig. 2). Total and average number of centric taxa at Drogomysl (19 and 7.75, respectively) were lower than at Goczalkowice (24, 10.83, respectively). *Cyclotella meneghiniana* and *Melosira varians* were the dominant centric taxa at Drogomysl, while *C. comta*, *C. pseudostelligera*, *Cyclostephanos dubius*, *Stephanodiscus hantzschii f. hantzschii*, and *S. hantzschii f. tenuis* were found more often and in greater numbers at Goczalkowice.

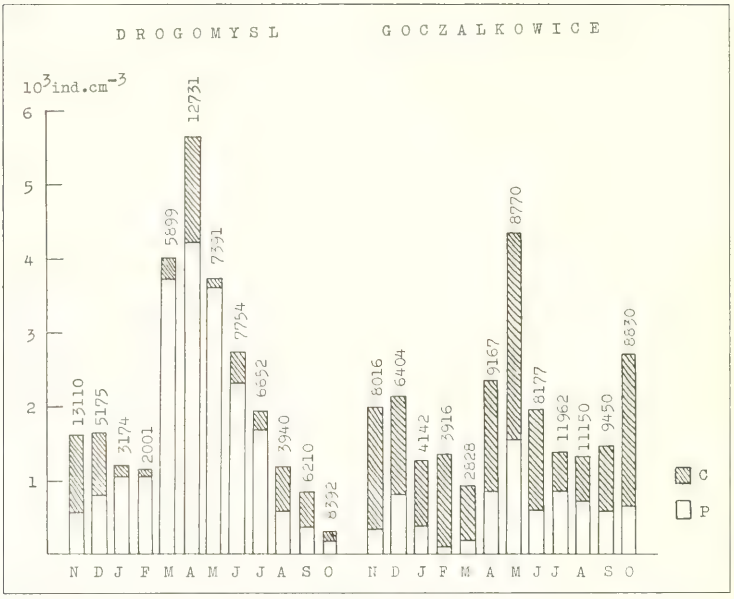


FIGURE 2. Monthly diatom densities in the River Vistula, 1982–83 (exact numbers on top of columns: all phytoplankton densities recorded as individuals cm^{-3}. C = centric diatoms, P = pennate diatoms.

The total number of species found at Drogomysl (78) was lower than that found at Goczalkowice (95) although the average number of pennate taxa at Drogomsyl (28.08) was higher than that found at Goczalkowice (23.75). Species such as *Cymbella silesiaca*, *C. sinuata*, *Diatoma hiemale*, *Fragilaria ulna* var. *acus*, *Gomphonema angustatum*, *Navicula gregaria*, *N. lanceolata*, and *Rhoicosphenia abbreviata* were found more often at Drogomysl. *Fragilaria pinnata* was more abundant at Goczalkowice. The number of pennate species increased upstream from the reservoir during the flood period (March and April, Fig. 3). Number of constant species (C = 4–5) was, for the centric taxa, 6 at Drogomysl and 9 at Goczalkowice, while the number of constant pennate species totaled 15 at Drogomysl and 10 at Goczalkowice. A total of 58 species were recorded as rare (C = 1–2) upstream from the reservoir at Drogomysl and 82 species were found to be rare downstream at Goczalkowice.

Quantitative differences in diatoms were found between upstream and downstream sites. Between November 1982 and February 1983 there were 1100–1600 individuals cm^{-3} upstream from the reservoir (Fig. 2). Pennate species consisted of 35–50 % of all diatoms between November and December, then rose to 88–94% by January–February. During the spring floods in March and April, number of individuals increased 4–5 fold, reaching a maximum in the middle of April (5640 individuals cm^{-3}). Number of individuals of pennate diatoms then decreased gradually, until the end of the growing season. Tychoplanktonic species dominated during this period and included *Achnanthes minutis-*

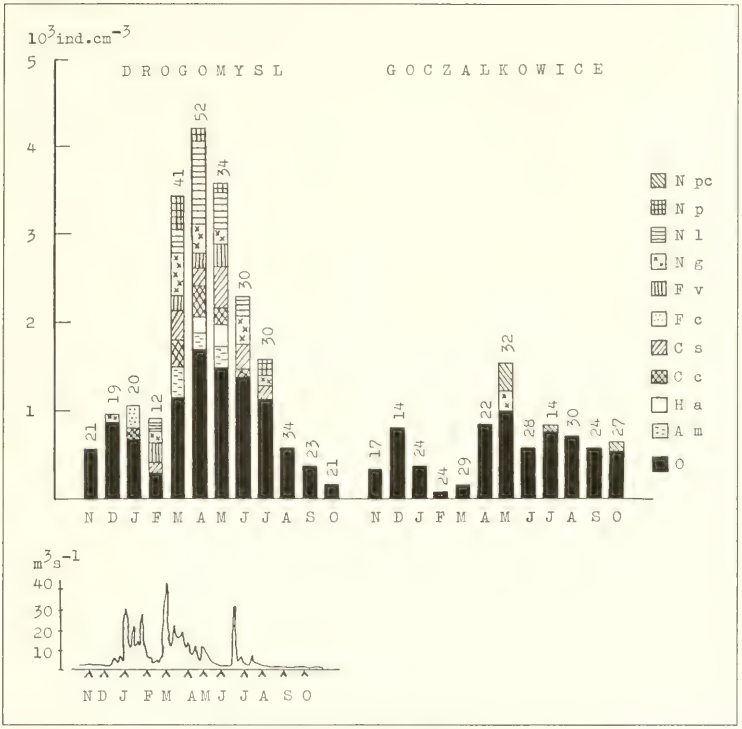


FIGURE 3. Quantitative changes of dominant pennate species in the River Vistula (large diagram), and water discharge (small diagram) at Drogomysl. Arrows at diagram of discharge show the exact day of sampling. Numbers on top of columns indicate numbers of species. O = other Pennates spp.; A m = *Achnantes minutissima*; H a = *Hannaea arcus*; C c = *Cymbella caespitosa*; C s = *C. silesiaca*, F c= *Fragilaria capucina*; F v = *F. capucina* var. *vaucheriae*; N g = *Navicula gregaria*; N l= *N. lanceolata*; N p = *Nitzschia palea*; N pc = *N. paleacea*.

sima, *Cymbella caespitosa*, *C. silesiaca*, *Fragilaria capucina* v. *vaucheriae*, *Hannaea arcus*, *Navicula gregaria*, *N. lanceolata*, and *Nitzschia palea*. These species numbered over 200 individuals cm^{-3}. It is worth noting that *Navicula lanceolata* comprised 17 % of the diatoms with a total of 955 individuals cm^{-3} in April. By the middle to the end of summer, after the floods, dominance of pennate species decreased and some centric species such as *Cyclotella meneghiniana*, *C. pseudostelligera*, and *Stephanodiscus minutulus* reached over 100 individuals cm^{-3}. A comparison of Figures 2 and 3 shows that, except for the low-water period at the end of the summer and autumn, pennate species dominated at the Drogomysl site.

Downstream from the reservoir, centric diatoms were usually found in greater numbers than pennates. Between November and February, *Cyclotella comta* was the dominant

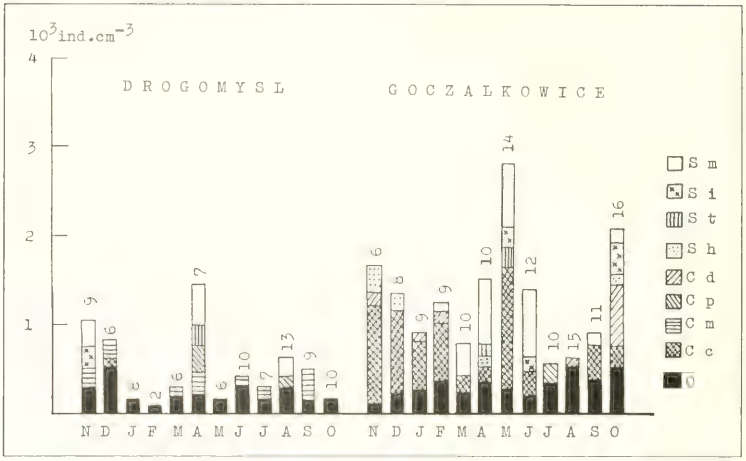


FIGURE 4. Quantitative changes of dominant centric species in the River Vistula. Numbers on top of columns indicate number of species. O = other Centrales spp; C c = *Cyclotella comta*; C m = *C. meneghiniana*; C p = *C. pseudostelligera*; C d = *Cyclostephanos dubius*; S h = *Stephanodiscus hantzschii f. hantzschii*; S t = *S. hantzschii f. tenuis*; S i= *S. invisitatus*; S m = *S. minutulus*.

species at this site, comprising 45–56 % of the community (575–1110 individuals cm^{-3}). *Cyclostephanos dubius*, *Stephanodiscus hantzschii f. hantzschii*, and *S. minutulus* each had over 100 individuals cm^{-3}. The only pennate taxon that occurred in greater numbers in the winter was *Achnanthes minutissima* (Table 1). The smallest number of algae occurred in March. Although there was still ice on the reservoir in March, it had melted by the middle of the month. Quick propagation of planktonic diatoms began in April and reached their peak in May. Numbers doubled over this period, caused by increases in the centric species *S. minutulus* and *C. comta* (Fig. 4). Other dominant species during this period included the centric taxa *S. invisitatus*, *S. hantzschii f. hantzschii*, *S. hantzschii f. tenuis*, as well as the pennate taxa *Achnanthes minutissima*, *Navicula gregaria*, and *Nitzschia paleacea*. The spring peak in numbers of individuals dropped by June and remained stable until October. The decrease was caused by a reduction in the numbers of *C. comta* cells. Between June and September diatoms consisted mainly of euplanktonic species, including the centrics and *Nitzschia acicularis*, *N. fruticosa*, *N. palea*, and *N. paleacea*. The peak in numbers in October is due to increases in centric species such as *Aulacoseira italica var. tenuissima*, *Cyclostephanos dubius*, *Cyclotella comta*, *Stephanodiscus invisitatus*, *S. hantzschii f. tenuis*, and *S. minutulus*.

Discussion

Relative to other published accounts of diatoms in Poland, the 79 diatom taxa found at Drogomysl are nearly seven times the number of taxa found by Kwadrans (1986) in the Biała Wiselka. This difference is due to the fact that Kwadrans investigated the diatoms of a small, quick-flowing mountainous river and did not report a single euplanktonic species.

Pajak (1986a), studying the phytoplankton of Wisla Czarne reservoir between 1981 and 1983, found more than 30 diatom species. Euplanktonic centric species dominated between May and September, and species reported by Pajak were also found at Drogomysl.

Regular study of the Goczalkowice Reservoir between 1955–1982 has resulted in the identification of 138 diatom taxa (Krzyzanek and Krzyzanek 1986; Krzyzanek et al. 1986; Pajak 1986b). Comparison of this taxonomic list with our own yields only 51 taxa are common. Of the taxa previously reported, 61 were not found in our study and a total of 87 taxa found in the present study have not previously been identified from the reservoir. Many of these newly reported forms are centric taxa, and possible oversight of them by previous investigators is due probably to the fact that electron microscopes were not available to former investigators. Thus, the suite of *Stephanodiscus* taxa were all previously identified as *S. hantzschii*.

We would like to deal with the morphological and taxonomical aspects of *Stephanodiscus minutulus* in detail. This species was found in great numbers mainly below the reservoir. A special form was found in summer and early autumn, which could be identified as *S. rugosus* Sieminska et Chudibowa, based on Sieminska and Chudibowa's work (1979), or as *Pseudostephanodiscus perforatus* (Genkal et Kuzmin) Sieminska, according to Sieminska (1988). We considered this special form to be *S. minutulus*. In the heavily silicified valves of this species, areolae are covered, so that they are hardly visible. According to Sieminska (1988), only "irregularly disposed rough chinks instead of radially arranged files of areolae" can be seen on scanning electron micrographs (Figs. 7, 8). We could not find on our specimens "a narrow dental frill on the abvalvar mantle edge of the valve" (Fig. 11), described by Sieminska (1988). The LM and SEM study of the Lake Dragow population by Casper et al. (1988) also led to the conclusion that *S. rugosus* is identical with *S. minutulus*.

If we analyze Sieminska's TEM pictures (1988) and our own micrographs (Figs. 5, 6), it can be clearly seen that the areola pattern is the same for *S. minutulus* and *S. rugosus*. The radially arranged rows of areolae divide into two or three rows near the margin and are covered with a thin siliceous layer, which is irregularly perforated over the areolae. The covered structure and the little spikes at the edge of the valve are caused by heavy silification and cannot be considered a general morphological characteristic that could justify its separation into another genus or as an independent species.

For these reasons we consider *Stephanodiscus rugosus* and *Pseudostephanodiscus perforatus* as synonyms of *S. minutulus*. We agree with Sieminska's statement (1988) that the morphological characteristics of *Stephanodiscus perforatus* Genkal et Kuzmin are the same as those she described as *S. rugosus*. Therefore, *S. perforatus* also is a synonym for *S. minutulus*.

Quantitative changes of the Vistula's phytoplankton, especially the diatoms, flowing into the reservoir were compared with the changes of water discharge. We found that changes in discharge strongly influence the quantity of diatoms. The most pronounced instance of this phenomenon was in March where, after a month-long period of low water, water levels quickly rose in the first days of the month. The flood peaked on March 10, the day of our sampling (Fig. 3). Instead of the expected low algal numbers that are typical in early spring, we found 5900 individuals cm^{-3}. Samples contained 62 % of periphytic pennate species including *Hannaea arcus*, *Navicula lanceolata*, *Cymbella*, *Gomphonema*, and *Surirella* (Table 1). It is obvious that this increase was caused by the high speed and great turbulence of the water washing off tychoplanktonic algae from the periphyton into the plankton. Another instance could be noticed on April 13. In a decreasing discharge

period after the flood series that began in March, a typical spring phytoplankton bloom developed in the gradually warming water. Besides centric species, *Asterionella formosa*, *Nitzschia acicularis*, and several Chlorococcales species had over 100 individuals cm^{-3}. The lowering water level, reduced flow, and warmer and more transparent water provided good conditions for the formation of the spring bloom, as described for other European rivers, (e.g., Kiss and Nausch 1987; Kuzmin 1979; Schmidt and Vörös 1981; Swale 1964).

Quantitative changes of diatoms downstream from the reservoir is dominated by lacustrine features. Ice over the reservoir melted by the middle of March. These melts are followed by a phytoplankton bloom in which the dominant species are centric. These diatoms are most abundant in May and decreased in number thereafter. After this, diatom numbers were reduced relative to Chlorococcales and Cyanophyta species (Pajak and Kiss 1990). Samples from Goczalkowice show great similarity to the phytoplankton of the eutrophic Keszhely Bay of Hungary's Lake Balaton (Kiss and Padisàk 1990).

We can conclude that the Goczalkowice Reservoir influences the taxonomic composition and quantitative relations of the Vistula's phytoplankton and diatom communities. Upstream from the reservoir the effect of changing discharge, like floods and low-water periods, can be observed on the diatoms. In floods the number of tychoplanktonic, periphytic pennate species are significantly increased. In low-water periods euplanktonic species are dominant, which is characteristic of the middle stretch of large European rivers. Increases in the number of euplanktonic species in the Wisla-Czarne Reservoir during this period may also play an important role. Downstream from the Goczalkowice Reservoir the river does not show the mountainous upper-stretch characteristics. Rich phytoplankton is formed in the reservoir over the growing season, and the Vistula's planktonic diatom communities show several features that are characteristic of eutrophic lakes.

Literature Cited

CABEJSZEK, I., Z. MALANOWSKI, AND J. STANISLAWSKA. 1959. Seston rzek Wisly na odcinku Góra Kalvaria-Plock. Polskie Archiwum Hydrobiologii 5:29–37.

CASPER, S. J., W. SCHEFFLER, K. AUGSTEN, AND T. PESCHKE. 1988. Some observations on the *Stephanodiscus hantzschii*-group (Bacillariophyta) in waters of the GDR. III. *Stephanodiscus delicatus* and *S. rugosus* in Lake Dragow. Limnologica 19:27–34.

HANAK-SCHMAGER, M. 1974. Seston i peryfiton rzek Wisley na odcinku od Nowego Bierunia do stopnia wodnego w Laczanach oraz Kanalu Laczany-Skawina. Acta Hydrobiol. 16:345–365.

KISS, K. T. 1986. Species of the Thalassiosiraceae in the Budapest section of the Danube. Comparison of samples collected in 1956–63 and 1979–83. Pp. 23–31 *in* Proceedings of the 8th International Diatom Symposium, M. Richard, ed. O. Koeltz, Koenigstein.

KISS, K. T. AND M. NAUSCH. 1987. Phytoplanktonuntersuchungen an ausgewählten äuerprofilen der Donau bei Klosterneuburg und Göd. 26. Arbeitstagung der IAD. Passau/Deutschland. Pp. 379–383.

KISS, K. T. AND J. PADISÀK. 1990. Species succession of Thalassiosiraceae: Quantitative studies in a large, shallow lake (Lake Balaton, Hungary). Pp. 481–490 *in* Proceedings of the 10th International Diatom Symposium, H. Simola, ed. O. Koeltz, Koenigstein.

KLIMOWICZ, H. 1981. The Plankton of the River Vistula in region of Warsaw in the years 1977–1979. Acta Hydrobiol. 23:47–67.

KUZMIN, G. V. 1979. Algae: A. Phytoplankton of the Volga. Pp. 137–170 *in* The River Volga and its life, D. Mordakhai-Boltovski, ed. Junk Publishers, The Hague.

KRZYZANEK, E., H. KASZA, W. KRZANOWSKI, T, KUFLIKOWSKI, AND G. PAJAK. 1986. Succession communities in the Goczalkowice dam reservoir in the period 1955–1982. Arch. Hydrobiol. 106:21–43.

KYSELOWA, K. AND A. KYSELA. 1966. Seston, peryfiton i mikrobentos Wisly od Oswiecimia do Krakowa. Acta Hydrobiol. 8, Suppl. 1:345–387.

KWADRANS, J., 1986. The structure of a diatom community in the spring sector of a stream with low pH (Biala Wiselka, Silesian Beskid Polan). Acta Hydrobiol. 28:139–148.

LUND, J. W. G., C. KIPLING, AND E. D. LE CREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiol. 11:143–170.

PAJAK, G. 1986a. The phytoplankton in the Wisla-Czarne reservoir on the years 1981–1983. XIII. Zjazd Hydrobiologow Polskich, Szczecin: 155–156.

———. 1986b. Development and structure of the Goczalkowice Reservoir ecosystem. VIII. Phytoplankton. Ecologia Polska 34:397–413.

PAJAK, G. AND K. T. KISS. 1990. Seasonal changes of phytoplankton in Vistula River, above and below the Goczalkowice Reservoir. Acta Hydrobiologica 32:101–114.

SCHMIDT, A. AND L. VÖRÖS. 1981. A Duna magyarországi alsó szakaszának fitoplanktonja az 1970-es években. Hidrolgiai Közlöny 61:322–330.

SIEMINSKA, J. 1988. *Pseudostephanodiscus* gen. n. (Bacillariophyceae). Arch. Protistenk. 135:183–185.

SIEMINSKA, J. AND D. CHUDYBOWA. 1979. *Stephanodiscus rugosus* Siem. et Chud. sp. n. (Bacillariophyceae) found in waters of the Mazurian Lake District in Poland. Frag. Flor. Geobot. 25:459– 463.

SWALE, E. M. F. 1964. A study of the phytoplankton of a calcareous river. J. Ecol. 52:433–446.

TUROBOYSKI, L. 1962. Wstepne badania nad wystepowaniem okrzemek w Wisle w Krakowie. Ekologia Polska 10:273–284.

TYSZKA-MACKIEWICZ, J. 1983. Bioseston i peryfiton rzeki Wisly na odcinku od Pulaw do Warszawy. Poznaskie Towarzystwo Przyjaciol Nauk. Wydzial Matematyczno-Przyrodniczy Prace Komisji Biologicznej 63:1–109.

UHERKOVICH, G. 1970. Über das Wisla-Phytoseston zwischen Kraków und Tczew. Acta Hydrobiol. 12:161–190.

WYSOCKA, H. 1950. Glony Wisly na odcinku Warszawy, I. Seston. Acta Soc. Bot. Poloniae 20:69–118.

TABLE 1. Quantitative changes of diatoms in four characteristic samples. J = January; M = March; M = May; O = October; c = constancy value of species; x = species found in other month; * = new species among the reservoir's flora.

	Drogomyśl					Goczalkowice				
	J	M	M	O	C	J	M	M	O	C
Aulacoseira ambigua (O.Müll.)Sim.*								x		1
A. distans var. *alpigena* (Grun.) Sim.*	x		100	20	4	x	10	x	105	5
A. granulata var. *angustissima* (O. Müll.) Sim.				x	1				35	1
A. italica var. *tenuissima* (Grun.) Sim.*	15		x	x	2	x	x	x	160	4
Cyclotella atomus Hust.*		x	x	x	3				35	2
C. caspia Grun.*		x		x	1				x	1
C. comta (Ehr.) Kütz.	15	x	x	20	4	575	195	1365	250	5
C. cryptica Rein., Lewis et Guill.*			x		1					
C. glomerata Bachm.*								x		1
C. meneghiniana Kütz.	15	110	25	20	5			x	x	3
C. pseudostelligera Hust.*	15	x	x	x	3	70	10	55	35	5
C. stelligera Cleve et Grun.*	x			20	1	x	x	30	x	2
Cyclostephanos dubius (Fricke) Round*						115	20	55	710	5
Melosira varians C. A. Agardh	40	110	30	x	5	x	20	30	x	4
Skeletonema potamos (Weber) Hasle*									x	1
Stephanocostis chantaica Genk. et Kuzm.*				x	1					
Stephanodiscus binderanus (Kütz.) Krieg.*								x		1
S. delicatus Genkal*									x	1
S. hantzschii Grun. f. *hantzschii*		x			1	x	65	85	105	5
S. hantzschii f. *tenuis* (Hust.) Håk. et Stoerm.*		x	x	10	2	20	35	220	70	3
S. invisitatus Hohn et Hellerman*	15	55	30	15	4	25	35	225	55	5
S. minutulus (Kütz.) Cleve et Möller*	15	x	55	15	5	95	360	755	175	
S. rotula (Kütz.) Hendey*	10			1		10	x	x	2	
S. triporus Genkal et Kuzmin*								x	x	1
Thalassiosira guillardii Hasle*				x	1					
Th. pseudonana Hasle et Heim.*			x	x	2			x	35	3
Th. weissflogii (Grun.) Fryx. et Hasle*								x		1
Total Centrales	130	275	240	125		900	760	2820	1770	
Achnantes affinis Grun.*			x		1	x			30	2
A. austriaca Hust.*		30	55		2	10	5			2
A. bioreti Germain*		x	x	x	2	5	x		x	2
A. clevei Grun.*				x	1		x	x		1
A. conspicua A. Mayer*							x			1
A. delicatula Kütz.*	x	95	140	x	4	x	x	x	15	3
A. exigua Grun.*									15	1
A. hungarica Grun.*	x		55		2	x			x	1
A. lanceolata (Bréb.) Grun.		95	x	x	3	40	10	30	15	4
A. linearis (W.Smith) Grun.								x	80	2
A. minutissima Kütz.	x	375	225	10	5	80	15	90	x	5
A. saxonica Krasske*		30	110			2			x	45
Amphora ovalis Kütz.		95	x		2			x	x	1
A. pediculus Kütz.	25	25	10	3	5	10	30	15	4	
Asterionella formosa Hass.	x	x	x	x	3			x	x	2

TABLE 1, continued.

	Drogomysl					Goczalkowice				
	J	M	M	O	C	J	M	M	O	C
Caloneis silicula (Ehr.) Cleve				x	1		x			1
Cocconeis pediculus Ehr.	x	x	55	5	5	x			x	1
C. placentula Ehr.	50	30	x	4	5	x	30	x	3	
Cymatopleura elliptica (Bréb.) W. Smith		x	110		1				x	1
Cymbella caespitosa (Kütz) Brun*	130	310	190	x	4	5		30	x	2
C. cistula (Ehr.) Kirch.							x			1
C. prostrata (Berkeley) Grun.						x				1
C. silesiaca Bleisch in Raben	50	315	470	5	5	20	5	60	15	4
C. sinuata Gregory	x	x	110	x	5	x			x	1
C. turgidula Grun.*	80	x	x	2						
Diatoma elongatum (Lyngbye) Agardh							x	30		2
D. elongatum var. *actinastroides* Krieg.*							x	x		1
D. elongatum var. *tenue* (Ag.) V. Heurk*		30			1			x		1
D. hiemale (Lyngb.) Heiberg	x	x	195	x	3		x	x		1
D. hiemale var. *mesodon* (Ehr.) Fricke*		x			1					
D. vulgare Bory	x	60	x		2				15	1
Diploneis ovalis (Hilse) Cleve							x	x		2
Eunotia exigua (Bréb.) Raben.							x			1
E. lunaris (Ehr.) Bréb.							x	x	x	2
E. tenella (Grun.) Hust.*						x	x			1
Fragilaria brevistriata Grun.*							5			1
F. capucina Desm.	270	30	50	x	3		x	60	x	3
F. capucina var. *vaucheriae* (Kütz.) Lange-Bert.	x	185	250	5	5	15	5	x	45	5
F. construens (Ehr.) Grun.*	x	x	x	x	3	5		30	15	2
F. construens var. *binodis* (Ehr.) Grun.*								x		1
F. construens var. *subsalina* Hust.*								x		1
F. crotonensis Kitton		x	80		1					
F. pinnata Ehr.*	x			x	1	30	x	30	30	5
F. ulna (Nitzsch) Lange-Bert.	55			10	2		x			1
F. ulna var. *acus* (Kütz.) Lange-Bert.	x	x	85	5	4	x	5	120		3
F. ulna var. *goulardii* (Bréb.) Lange-Bert.	25		30	x	2		5		x	1
Gomphonema acuminatum Ehr.						x				1
G. angustatum (Kütz.) Raben.	x	125	55	x	4	5	x	30	x	3
G. angustum Agardh*		30	x		2	10		x	x	2
G. clavatum Ehr.		x			1		x			1
G. minutum (C.Agardh) C.Agardh*		x			1					
G. olivaceum (Horn.) Bréb.*	x	30	x	x	3	5	x		x	2
G. olivaceum car. *minutissimum* Hust.*		x			1					
G. parvulum Kütz		60	x	x	2	5			15	2
G. truncatum Ehr.*		x			1	5				1
Gyrosigma acuminatum (Kutz.) Raben.								x		1
G. attenuatum (Kütz.) Cleve*						x				1
Hannaea arcus Ehr.	x	95	250	5	4			30	x	1
Meridion circulare (Grev.) Agardh		x		x	1			x		1

TABLE 1, continued.

	Drogomysl					Goczalkowice				
	J	M	M	O	C	J	M	M	O	C
Navicula atomus var. *excelsa* (Krasske) Lange-Bert.*		x			1					
N. capitata Ehr. var. *capitata*		x			1					
N. capitata var. *hungarica* (Grun.) Ross	x		x	5	3		x	x	x	2
N. capitatoradiata Germain*		x			1		x			1
N. costulata Grun. in Cleve & Grun.*								x		1
N. cryptocephala Kütz.	130	45	x	30	5	55	15	30	45	5
N. goeppertiana (Bleisch) H.L. Smith*						x	x			2
N. gregaria Donkin*	35	500	190	10	5	x	25	220	x	5
N. halophila (Grun.) Cleve*						x		60		1
N. hambergii Hust.*		x			1					
N. ignota Krasske*		x			1					
N. lanceolata (Agardh) Ehr.	80	250	420	10	5	x	5	x	x	3
N. menisculus Schumann*		x	25	x	2		x	x	15	2
N. minima Grun.*		x			1					
N. perminuta Grun.*							x			1
N. pupula Kütz.						5	x	30	x	2
N. rhynhocephala Kütz	x				1	x	x		x	2
N. saprophila Lange-Bert. & Bonik*									x	1
N. slesvicensis Grun.*		x			1					
N. subminuscula Manguin*		x			1					
N. tripunctata (O.F. Müller) Bory*		x		5	2	x	x	x	15	3
N. trivialis Lange-Bert.*		x			1					
N. viridula var. *rostellata* (Kütz.) Cleve							x			1
Nitzschia acicularis (Kütz) W.M. Smith*	x	x	x	x	3	x		60	x	3
N. amphibia Grun.*		x			1					
N. angustatula Lange-Bert.									x	1
N. capitellata Hust. in A. Schmidt et al*		125	85		3					
N. clausii Hantzsch*									x	1
N. dissipata (Kütz.) Grun.*		60	x	x	3	15	10	90	x	4
N. fonticola Grun.*	x	x	x	x	3					
N. fruticosa Hust.*								x	x	1
N. heufleriana Grun.*	x				1					
N. intermedia Hantzsch*	x				1					
N. levidensis (W. Smith) Grun. var. *levidensis*								x		1
N. linearis (Aghard) W. Smith	25	x	55	x	3		5	30	x	2
N. palea (Kütz.) W. Smith	55	410	110	20	5	5	5	x	60	4
N. paleacea Grun.*	x	x		x	3			345	110	3
N. pusilla (Kütz.) Grun.*		x			1	5				1
N. recta Hantzsch in Raben.*							x	x		1
N. sinuata var. *tabellaria* Grun.*						10				1
N. sublinearis Hust.*		x			1					
N. trylionella Hantzsch*				x	1			x		1
N. vermicularis (Kütz.) Hantzsch*						x			x	1
Pinnularia interrupta W.M. Smith							x			1

TABLE 1, continued.

	Drogomysl					Goczalkowice				
	J	M	M	O	C	J	M	M	O	C
Rhoicosphenia abbreviata (C.Agardh) Lange-Bert.	25	30	x	x	3			x	x	1
Stauroneis anceps Ehr.				5	1		10	x		2
Surirella angustata Kütz.*		x	x		2					
S. biseriata Bréb. et Godey*							x			1
S. brebissonii Krammer et Lange-Bert.		90	110		2					
S. minuta Bréb.*		95	30		3		5	85		2
S. robusta Ehr.		125	x		2	x		x	x	2
Tabellaria flocculosa (Roth) Kütz.		x			1					
Total Pennales	1035	3720	3595	140		345	145	1550	595	
Total diatoms ind cm^{-3}	1165	3995	3835	265		1245	905	4370	2365	

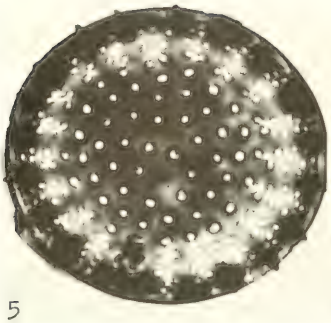
Explanation of Plates

Plate 1, Figures 5–10

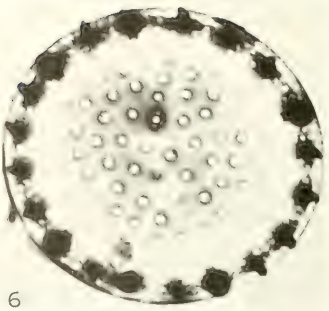
FIGURES 5–10. *Stephanodiscus minutulus*. FIGURES 5, 6. TEM structure of the valve showing the "normal *minutulus*" areola pattern. FIGURES 7-10. SEM. FIGURES 7, 8. External view of the valve face with the irregularly perforated, thin silica layer. External tube of the labiate process is indicated in Fig. 8 (arrow). FIGURES 9, 10. Internal view of the valve face showing the areola pattern and different types of processes. Scale bars = 5 μm.

Plate 2, Figures 11–16

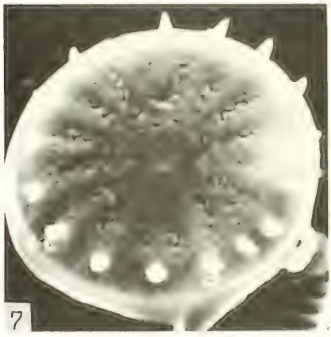
FIGURES 11-15. SEM. FIGURE 11. *Stephanodiscus minutulus* in lateral view with the large spines. FIGURE 12. *Cyclostephanos dubius* in lateral view. FIGURE 13. *Cyclotella comta*. FIGURE 14. *Stephanodiscus rotula*. FIGURE 15. *Stephanodiscus delicatus*. FIGURE 16. *Stephanocostis chantaica* showing the TEM structure of valve face with the large ribs. Scale bars = 5 μm.



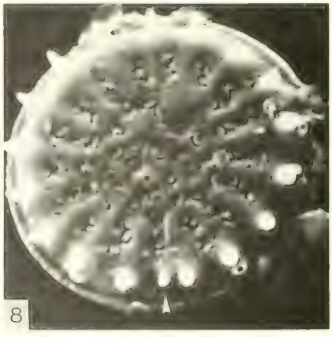
5



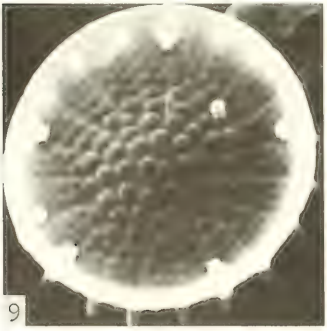
6



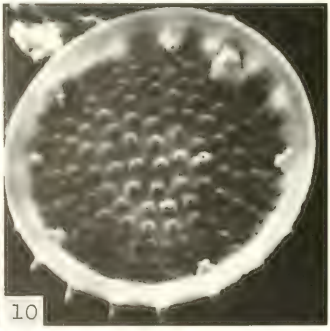
7



8



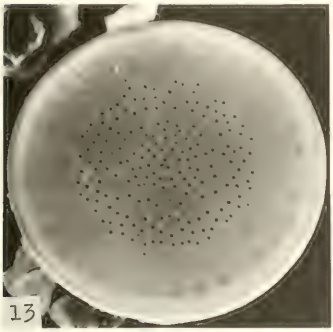
9

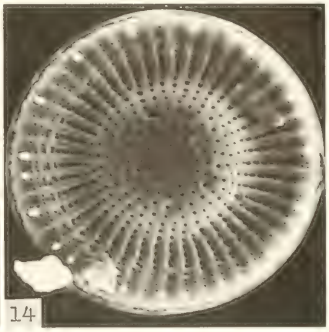


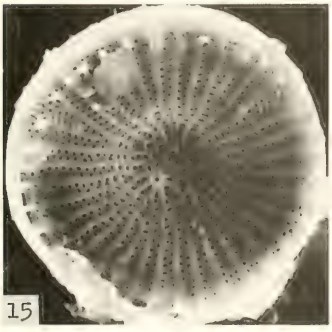
10

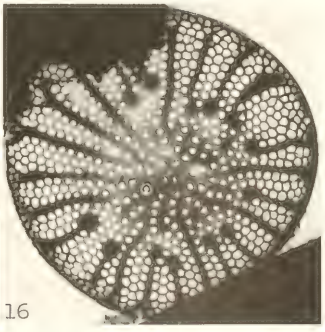
11

12


13


14


15


16

Effects of Grazing by the Trichopteran, *Glossoma nigrior*, on Diatom Community Composition in the Ford River, Michigan

by

Thomas M. Burton

Departments of Zoology and Fisheries and Wildlife,
Michigan State University, East Lansing, Michigan 48824

and

Mark P. Oemke and Jennifer M. Molloy

Department of Zoology, Michigan State University,
East Lansing, Michigan 48824

with 4 tables

Abstract: Larvae of the trichopteran grazer, *Glossoma nigrior*, were exposed to diatom communities that had accumulated for 22–28 days on ceramic tiles in a fourth-order stream in several experiments conducted annually from 1985 through 1989. The plexiglass streams used in these experiments were situated on the stream bank and were subdivided into 12 separate study chambers. We evaluated the response of the periphyton community to three densities of *Glossosoma* larvae (0, 500, and 1000 m^{-2} corresponding to 0, low, and high local densities) with the three treatments randomly assigned to four chambers each in the first experiment in 1985. Thereafter, the experiments included only two treatment levels (0 and 1000 larvae m^{-2}). The diatom communities on the tiles were exposed to grazing for 6–7 days for all experiments except those in 1989, which lasted for 14 days. Grazing resulted in no consistent difference in chlorophyll a or in accumulation of organic matter biomass (AFDW) in any experiment. Grazing caused shifts in relative abundance of the diatom community in some years but not in others. Primary shifts occurred for the two dominant species with increases in *Achnanthes minutissima* abundance being accompanied by decreases in abundance of *Cocconeis placentula* when total diatom density was initially low. When total diatom density was initially high, dominance by *A. minutissima* decreased as a consequence of grazing. At intermediate levels of total diatom density, no significant shifts in dominance of the major species present occurred. The effects of grazing on total cell density also appeared to be related to initial cell density with grazing decreasing cell density when total diatom density was initially high but otherwise having no effect. Comparison of the diatoms in the grazer guts with the diatom communities on grazed tiles provided little evidence for selective predation by *Glossosoma*. Instead, grazing appeared to affect competition (perhaps for space) among the diatoms depending on the density of diatom cells initially present.

Introduction

Stream herbivores (grazers) can alter the structure of the attached algal community in freshwater streams (e.g., Colletti et al. 1987; Dickman and Gochnauer 1978; Eichenberger and Schlatter 1978; Hart 1985; Hershey et al. 1988; Hill and Knight 1987, 1988; Jacoby 1985; Kehde and Wilhm 1972; Lamberti and Resh 1983; Lamberti et al. 1987a, b; Peterson 1987; Power et al. 1988; Steinman et al. 1987; Sumner and McIntire 1982). Most research on grazer-algal interactions in streams has been for short time periods with high densities of grazers. Few such studies have been replicated at the same site for several years. We conducted studies on the influence of grazing by the fifth instar of the trichopteran, *Glossosoma nigrior* (Banks), on the diatom community in the Ford River in northern Michigan from 1985 through 1989. The objectives of these studies were to: (1) determine the impact of this important stream grazer on diatom community structure, and (2) to determine year-to-year variability in the impact of *G. nigrior* on the diatom community.

Materials and Methods

Experiments of grazer-diatom interactions were conducted in plexiglass streams located adjacent to riffles on the banks of the Ford River, a fourth order stream in Dickinson County in the upper peninsula of Michigan. The 1.27 cm thick plexiglass streams were 1 m long with three 15 cm wide channels fed from a common reservoir with water pumped from the river. Each channel was subdivided into four chambers by a 0.5 mm mesh plastic screen to prevent exchange of grazers between chambers. Water flow through these screens was relatively unimpeded. Water from the river was filtered through rolls of polyester and a 300 μm mesh screen in the common reservoir before flowing into the individual channels. The rolls of polyester and screen filtered excess sediment out of the water and kept sedimentation on the tiles in the chambers to a minimum. The plexiglass streams were located so that exposure to sunlight and shading by riparian vegetation was similar to that at the river surface. Temperature in the plexiglass streams was usually within two degrees of temperature in the river and varied between 15 and 22° C during the experiments.

Diatom assemblages similar to those on nearby rocks were obtained for the experiments by exposing ceramic tiles (3.6 cm^2) for 22–28 days on the stream bed to allow colonization (Oemke and Burton 1986).

After colonization, 20 tiles were selected and placed randomly in each chamber. The experiment was run in late July–early August 1985 at one site on the river using two densities of *Glososssoma* larvae (15 and 30 larvae per chamber) plus a control with no grazers present and repeated in September 1985 using 30 larvae per chamber and a no-grazer control. From 1986 through 1989, two experiments using 30 larvae per chamber and a no-grazer control were conducted simultaneously in late July or early August at two sites on the river approximately 8km apart.

The low density of 15 larvae per chamber simulated the estimated average density of 500 *Glososssoma* larvae per square meter in riffles in the Ford River where *Glososssoma* could easily be collected. The high density of 30 larvae per chamber simulated the 1000 larvae per square meter encountered at the most favorable sites. These densities in the river were estimated by picking up rocks over a square meter of riffle and counting the larvae encountered. All larvae used in the experiments were fifth instars collected from the river near the plexiglass streams. Those that had abandoned their stone cases or appeared to be dead were replaced daily with larvae collected from the river. Each experiment was

conducted for 6–7 days except in 1989 when duration of the experiment was extended to 14 days with a 7 day-intermediate sampling period.

Tiles were removed from each chamber at the conclusion of each experiment for determination of chlorophyll a (eight tiles per chamber), organic matter biomass (eight tiles per chamber) and for determination of algal species composition (four tiles per chamber). Organic matter biomass was not sampled in 1989, and 10 tiles each were removed after 7 days and 14 days (5 for diatom counts, 5 for chlorophyll determinations). The 7-day slides removed in 1989 were replaced with 10 pre-colonized slides to keep surface area exposed to grazing constant.

Slide preparations, diatom cleaning procedures, and microscope and calculation procedures are detailed in Oemke and Burton (1986). Since over 90 % of the total number of algal cells that developed on the tiles consisted of diatoms, no examination of green or blue-green algae was attempted.

Analyses for chlorophyll a and organic matter biomass followed *Standard Methods* (American Public Health Association 1985).

At the conclusion of each experiment, larvae from each treatment were preserved in a 60% water: 30% ethanol: 10% formalin solution. In 1985, five preserved larvae were selected from each of the treatment chambers for gut-content analysis. The number of diatom valves counted from slides from larval guts was at least 400 per slide rather than the 300 usually counted from tiles from the chambers to assure that equal numbers of diatoms were identified from the tile and larval gut slides.

Diatom community analyses between treatments and between experiments consisted of comparisons of measurements of species evenness (J′), species diversity (H′, Shannon-Weiner function), and the Similarity Index (SIMI). The SIMI index gives greater weight to the dominant rather than the rare taxa (Steinman et al. 1987)

A two-way nested analysis of variance model was used for significance testing between treatments for all parameters. Levels of significance are reported as $p \leq 0.05$ unless otherwise stated.

Based on appropriate geometric figures, individual biovolume was calculated from data on length, width, and thickness of frustules for over 20 of the most common species. Individual volume estimates were multiplied by the density of each species and summed to provide estimates of total biovolume.

Results

The 1985 experiments were the most detailed with changes in the diatom communities on the tiles and changes in the diatoms represented in the guts of *Glososoma nigrior* larvae examined, and with two levels of grazing included. Therefore, we will present results of the 1985 experiments and compare later experiments to these results. In 1985, significant shifts in species dominance occurred as a consequence of grazing. In the July experiment, the relative abundance of *Achnanthes minutissima* Kütz. increased significantly on grazed tiles under grazer densities of 15 and 30 larvae per chamber (Table 1). Grazing also significantly increased actual cell densities of *A. minutissima* for both grazed treatments compared to ungrazed controls. These results were repeated in the September 1985 experiment, since both relative abundance and actual cell density of *A. minutissima* increased significantly with grazing. *A. minutissima* was the most dominant species present on the control slides in September.

TABLE 1. Relative abundance (% of total valves counted) of diatom species commonly encountered in the 1985 experiments.

	Jul. – Aug. 30 larvae	Jul. – Aug. 15 larvae	Jul. – Aug. 0 larvae	Sept. 0 larvae	Sept. 30 larvae
*Achnanthes minutissima*Kütz.	26.54	31.73	14.34	39.70	60.90
Achnanthes lanceolata Bréb.*ex* Kütz.	2.10	1.02	2.24	2.75	2.43
Achnanthes linearis (W. Sm.) Grun.	3.28	1.38	2.24	1.98	1.80
Achnanthes deflexa Reim.	0.45	0.61	0.85	0.97	0.87
Amphora perpusilla (Grun.) Grun.	0.95	0.31	1.28	2.80	0.74
Cocconeis diminuta Pant.	0.31	0.29	0.27	0.64	0.30
Cocconeis pediculus Ehr.	2.64	2.18	2.23	0.53	0.08
Cocconeis placentula var. *euglypta* (Ehr.) Cl.	3.43	7.99	5.14	6.10	3.46
Cocconeis placentula var. *lineata* (Ehr.) V.H.	31.53	36.51	43.94	10.31	5.77
Cymbella minuta Hilse *ex* Rabh.	3.14	2.21	3.38	0.65	0.16
Fragilaria construens (Ehr.) Grun.	2.52	1.74	2.70	7.16	5.30
Fragilaria vaucheriae (Kütz.) Peters.	3.26	1.89	4.08	1.86	2.17
Gomphonema angustatum (Kütz.) Rabh.	1.89	0.41	0.94	1.54	1.75
Gomphonema dichotomum Kütz.	3.19	0.81	0.47	6.74	4.04
*Navicula decussis*Ostr.	0.21	0.51	0.36	0.30	1.29
*Navicula lagerstedtii*Cl.	0.76	0.66	0.47	0.79	0.30
Synedra ulna (Nitz.) Ehr.	0.59	0.27	0.66	0.19	0.47

The dominant diatom on ungrazed tiles in all late July–early August experiments was *Cocconeis placentula* Ehr. Its abundance declined as grazer density increased in the July 1985 experiment (Table 1), but this decline was not significant. This species was less common in the September 1985 experiment but again decreased in abundance as grazer pressure increased (Table 1).

Grazing had little impact on overall community structure in 1985, since SIMI comparisons between the communities on the grazed and ungrazed tiles were consistently above 0.9 for all comparisons in July and September. This index (0 = no species overlap, 1 = complete overlap) correlates communities based both on numbers of species present and the number of individuals of each species present.

The results for the diversity (H′) and evenness (J′) indices were inconsistent in the 1985 experiments (Table 2). In the July experiment, no significant differences occurred for either diversity or evenness between the ungrazed and grazed tiles at either grazer level. In the September experiment, grazing significantly lowered diversity and evenness on grazed tiles as compared to ungrazed tiles (Table 2).

Shifts in relative abundance due to grazing and the September decrease in diversity and evenness led us to question whether or not *Glossosoma* might be grazing selectively on diatoms. Diversity of diatoms sampled from gut contents of *Glossosoma* larvae in September were equal to diversities from grazed tiles but significantly lower than diversities determined from the ungrazed tiles (Table 2). Evenness for diatoms from grazer guts were also significantly lower than evenness from ungrazed tiles (Table 2). Thus, grazing by *Glossosoma* reduced the total number of diatom species present as well as altered the relative abundance of remaining species. However, results from the July experiment for the high grazer density were the reverse of those obtained in September with diatom diversity on both the ungrazed and grazed tiles significantly lower than diatom diversity in *Glossosoma* guts (Table 2). The SIMI index indicated high degress of overlap between

TABLE 2. Comparisons of species diversity (H′) and species evenness (J′) indices calculated from larval gut contents and diatoms on ceramic tiles exposed to three levels of grazer density. Values are means ± S.E.

Grazer density*	Diversity (H′) on tiles	Evenness (J′) on tiles	Diversity (H′) in guts	Evenness (J′) in guts
		July experiment		
0	2.23 ± 0.14	0.64 ± 0.03	—	—
15	1.89 ± 0.18	0.58 ± 0.11	2.43 ± 0.31	0.51 ± 0.04
30	2.12 ± 0.18	0.64 ± 0.11	3.48 ± 0.22	0.65 ± 0.03
		September experiment		
0	3.52 ± 0.08	0.68 ± 0.02	—	—
30	2.44 ± 0.29	0.53 ± 0.04	2.23 ± 0.09	0.50 ± 0.09

* = number of larvae per chamber; 15 = 500 larvae per m^{-2} or average number of larvae on rocks in erosional zones near the site of the experiment; 30 = 1000 larvae per m^{-2} or double the average number of larvae on rocks in erosional zones of the river.

TABLE 3. Ash-free dry weight organic matter biomass (AFDW), chlorophyll *a*, and diatom cell density levels measured from ceramic tiles exposed to different grazer densities. Values are means ± S.E.

Grazer density*	AFDW biomass ($mg \cdot m^{-2}$)	Chlorophyll a ($mg \cdot m^{-2}$)	Cell density ($Cells \cdot m^{-2} * 10^{-8}$)
		July experiment	
0	805 ± 66	3.40 ± 0.54	9.53 ± 1.73
15	757 ± 20	3.50 ± 0.49	12.99 ± 0.79
30	1,133 ± 117	3.47 ± 0.10	11.81 ± 2.40
		September experiment	
0	2,057 ± 260	1.92 ± 0.21	8.51 ± 2.38
30	945 ± 203	1.59 ± 0.16	9.02 ± 3.32

* = number of larvae per chamber; 15 = 500 larvae per m^{-2} or average number of larvae on rocks in erosional zones near the site of the experiment; 30 = 1000 larvae per m^{-2} or double the average number of larvae on rocks in erosional zones of the river.

diatoms in the guts and diatoms on the grazed and ungrazed tiles in September and in the low density grazer treatment in July, since all values were above 0.9 for these comparisons. However, the SIMI index was only 0.79 for the comparison between the diatoms in grazer guts collected from the high-density treatment in July and the diatom community on the grazed tiles, perhaps indicating some selectivity by the grazer after grazing had already altered diatom community structure on the tiles. The inconsistent results between the September and July experiments for diversity, evenness, and SIMI provide little evidence for diatom selectivity by the grazer. Diatom selectivity by the grazer should be reflected in lower species diversity in the guts than on the tiles, not the same or higher as was found in these two experiments. Selectivity should result in lower SIMI values between the community on the ungrazed tiles and diatoms found in the grazer guts. This result was obtained only for the high-grazer treatment in July.

The shift in 1985 towards greater dominance by *Achnanthes minutissima* on the grazed tiles with a concomitant, though non-significant, decrease in *Cocconeis placentula* appeared to be repeated in 1986 at the two sites studied. However, increases in relative abundance of *A. minutissima* were only significant at the $p > 0.10$ level and the decreases in abundance of *C. placentula* were not significant (Table 4). In 1987, grazing had no significant effect on the relative abundances of *A. minutissima* and *C. placentula* or on the relative abundance of the two other most common species of diatoms (*A. linearis* (W. Sm.) Grun. and *Gomphonema parvulum* (Kütz.) at either of the two study sites (Table 4). In 1988 and 1989, significant shifts had occurred by the end of the experiments in the relative abundance of five (1989) or six (1988) of the most common taxa, but the primary shift towards decreased dominance by *A. minutissima* in 1988 and 1989 is just the opposite of results obtained in 1985 and 1986 when dominance by this species increased on the grazed tiles. The consistently decreased dominance by *A. minutissima* on the grazed tiles in 1989 recorded after 14 days was less obvious after seven days exposure, with one site characterized by significant decreases but not the other. Likewise, the longer 14-day exposure to grazing in 1989 resulted in significant decreases in relative abundances of *C. placentula*, *A. linearis*, *Cymbella minuta Hilse ex* Rabh., and *Fragilaria brevistriata* Grun. between the grazed and ungrazed tiles, whereas the differences were significant only for *A. minutissima* and *Cocconeis placentula* after seven days exposure. Thus, extension of time of exposure to grazing from 7 days to 14 days led to results similar to those obtained after only 7 days in 1988 when grazing resulted not only in significant differences between grazed and ungrazed tiles for *A. minutissima* and *C. placentula*, but also for *A. linearis*, *Cymbella minuta*, *Fragilaria vaucheriae* (Kütz.) Peters., and *Gomphonema parvulum*.

In all of the one-week experiments conducted in late July–early August from 1985 through 1989, there were never any significant differences in diversity between the grazed and ungrazed tiles (Table 4). Grazing led to a significant decrease in diversity after two weeks exposure in 1989 and after one week exposure in the September, 1985 experiment. Evenness was significantly decreased by grazing in the September, 1985 experiment and in the 1986 experiments; however, grazing had no significant effect on evenness in the July–August experiments conducted in 1985, 1987, or 1989 (Table 4).

In the July and September, 1985 experiments, no level of grazing resulted in any significant impact on either total diatom cell density or standing crop of chlorophyll a on the tiles (Table 3). Likewise, grazing had no significant impact on total diatom biovolume or average diatom cell volume for any treatment or experiment. However, total accumulation

TABLE 4. Effects of grazing by *Glossosoma nigrior* (30 larvae/chamber) on the diatom community in the late July – early August experiments. All experiments were run for seven days except the 14-day 1989 experiment. NS = no significant change according to an analysis of variance. If changes were significant ($p > 0.05$), the direction of change is indicated with a + (= significant increase) or a –.

Year	Chl. *a*	AFDW	Density	Diversity	Evenness	*A. min.*	*C. pla.*
1985	NS	+	NS	NS	NS	+	NS
1986	NS	NS	NS	NS	–	+	NS
1987	NS	NS	NS	NS	NS	NS	NS
1988	NS	NS	–, NS	NS	NS	–	NS, +
1989							
7 Day	NS	– – –	–	NS	NS	–, NS	NS, +
14 Day	NS	– – –	–	–	NS	–	NS, –

* = results from two separate sites; if the two sites differed, the upstream site is listed first; otherwise, the results were the same for both sites. Chl. *a* = chlorophyll *a*, AFDW = accumulation of organic mater on the substrates expressed as ash free dry weight, Density = total diatom cell density, Diversity = Shannon Wiener diversity (H'), Evenness = Simpson's evenness, *A. min.* = percent dominance by *Achnanthes minutissima*, *C. pla.* = percent dominance by *Cocconeis placentula*

of organic matter expressed as ash-free dry weight (AFDW) was impacted by the high-grazer density treatments in both July and September, 1985 with a significant increase in July and a significant decrease in September (Table 3). These inconsistent results may have occurred because of very different amounts of organic matter on the control tiles (Table 3). The tiles in the September experiment had an AFDW biomass that was more than twice that of the tiles used in the July experiment. Replication of the late July–early August experiment at the higher grazer density each year from 1986 through 1989 never resulted in any significant difference in accumulation of AFDW organic matter biomass on the slides or in standing crop of chlorophyll a. Likewise, grazing led to consistently significant differences in cell density between the grazed and ungrazed tiles only in the the 1989 experiment when cell density was lowered by grazing (Table 4). There were no significant differences in cell density between treatments for any other experiment conducted from 1985 through 1988 except for a significant decrease at only one of the two sites studied in 1988 (Table 4).

Discussion

No single parameter measured for the diatom communities consistently changed in these experiments as a consequence of grazing. The effects of grazing on the community-based parameters H' and J' followed no specific pattern except that when changes occurred; they were in a negative direction. Grazing had little effect on chlorophyll a standing crop or on accumulation of AFDW organic matter on the tiles.

Relative abundance of the dominant species shifted for some or all of the experiments in 1985, 1986, 1988, and 1989. These shifts were only significant in 1986 at the $p > 0.10$ level and did not occur in 1987. The shifts were towards increased dominance by *A. minutissima* in 1985 and 1986 and decreased dominance by this species in 1988 and 1989. The magnitude and direction of these shifts may be related to the initial total cell densities

of the diatoms with shifts towards increased dominance by *A. minutissima* at low overall diatom cell density, no shift at intermediate levels, and shifts towards decreased dominance by *A. minutissima* at high initial diatom cell densities. In the 1985 experiments, cell densities on the ungrazed tiles were lower than in any other year ($9.5 \pm 1.7*10^8$ and $8.5 \pm 2.4*10^8$ cells m^{-2}, respectively), were highest in 1986 and 1989 ($92\text{-}177*10^8$ cells m^{-2}), and were intermediate in 1987 and 1988 ($29\text{-}56*10^8$ cells m^{-2}). The 1986 data do not fit a response related to initial total cell density. The tiles used in the 1986 experiment were not cleaned every few days during the colonization period, and silt and organic matter had become quite dense by the start of the grazer experiment. Organic matter on the tiles for the 1986 experiment was about 10-fold higher than for any other experiment. For all experiments after 1986, silt was lightly brushed off the tiles twice per week during colonization to limit this build up of silt and organic matter, since such a build up did not happen on the rocks in the river where the grazer was collected and the grazer appeared to have difficulty handling this situation. If we eliminate the 1986 results, the shifts in dominance along the response curve described above seem to apply as follows: Grazing shifts dominance toward *A. minutissima* at initial diatom densities less than $10*10^8$ cells m^{-2}, causes no shifts in dominance at intermediate levels of initial diatom cell densities of 29 to $31*10^8$ cells m^{-2} (experiments at both sites in 1987), and causes shifts towards decreased dominance by *A. minutissima* at initial total diatom densities of $44*10^8$ cells m^{-2} or higher (slight but significant shift at one of the two sites studied in 1988 occurred at this level with initial cell densities of $56*10^8$ cells m^{-2} in 1989 significant decreases occurred with initial cell densities of 134 to $142*10^8$ cells m^{-2}).

If the 1986 experiment is eliminated from consideration, the threshold effect for impact of grazing on total cell density appears to occur at levels between 44 and $56*10^8$ cells $.m^{-2}$. Grazing caused a significant decrease in cell density at the site in 1988 with the higher of these two values but not the other and at both sites studied in 1989. Grazing decreased total diatom densities when initial densities exceeded the threshold.

The mechanism for the shifts in relative abundance in the diatom community is unclear, but it may be a function of competitive interactions among the different species of diatoms. Our data on the diatoms in the gut contents of the grazer do not support selectivity by the grazer having much impact on community structure. Ingestion of *A. minutissima* and *C. placentula* in proportions roughly equal to their occurrence in the surrounding periphyton means that changes in species abundance on the grazed tiles following grazing activity must have resulted from some advantageous biological abilities of one of the diatoms. These could have included: (1) faster colonization, (2) faster growth and reproduction, (3) greater survivability in the grazer gut, or (4) less susceptibility to removal from substrates. In a separate study of diatom colonization, Oemke and Burton (1986) found that *Achnanthes* had colonization rates equal to or less than those of *Cocconeis* on uncolonized substrates. This would seem to rule out faster colonization as a means for *Achnanthes* to increase in proportion. *Glossosoma* seems to have little difficulty in removing adnate forms such as *Cocconeis* and *Achnanthes* as has been reported for other grazers (Patrick 1970; Moore 1975, 1977a, b). Scanning electron microscopy of summer communities from this river shows that the flora consists of a matrix of *Cocconeis* cells with *Achnanthes* cells interspersed in the matrix. *Cocconeis* is usually found with one entire valve surface fully attached to the substrate, while the smaller *Achnanthes* often grows attached at one end only. It is difficult to visualize a grazer being able to selectively remove one of these species from the interspersed matrix. Thus, differential susceptibility to predation for these two species seems unlikely. In their studies of *Cocconeis* and *Achnanthes*, Brown and Austin (1973) found that whichever became established first usually became dominant. In the present study, the effects of grazing appeared to change the

variable outcome of competition for substrate space between these two diatom species into a consistent victory favoring *A. minutissima* at low initial total diatom cell densities and into a consistent victory favoring *C. placentula* at high initial total cell densities. Different growth and reproductive rates of the diatoms under these different conditions would seem to be the most logical explanation for these observations.

Acknowledgements

We would like to thank Mike O'Malley and Dennis Mullen for technical assistance. Karl Ulrich aided in design and building of the artificial streams. Support for this research was provided by the U. S. Naval Electronic Systems Command through a subcontract to Michigan State University from IIT Research Institute under Contract N00039-84-C-0070.

Literature Cited

AMERICAN PUBLIC HEALTH ASSOCIATION. 1985. Standard Methods for the Examination of Water and Wastewater. 16th edition, American Public Health Association, Washington, D. C. 1268 pp.

BROWN, S. D. AND A.P. AUSTIN. 1973. Diatom succession and interaction in littoral periphyton and plankton. Hydrobiologia 43:333–356.

COLLETI, P. J., D. W. BLINN, A. PICKART, AND V. T. WAGNER. 1987. Influence of different densities of the mayfly grazer *Heptagenia criddlei* on lotic diatom communities. J. N. Am. Benthol. Soc. 6:270–280.

DICKMAN, M. D. AND M. B. GOCHNAUER. 1978. A scanning electron microscope study of periphyton colonization in a small stream subjected to sodium chloride addition. Verh. Int. Verein. Theor. Angew. Limnol. 20:1738–1743.

EICHENBERGER, E. AND A. SCHLATTER. 1978. The effect of herbivorus insects on the production of benthic algal vegetation in outdoor channels. Verh. Int. Verein. Theor. Angew. Limnol. 20:1806–1810.

HART, D. D. 1985. Grazing insects mediate algal interactions in a stream benthic community. Oikos 44:40–46.

HERSHEY, A. E., A. L. HILTNER, M. A. J. HULLAR, M. C. MILLER, J. R. VESTAL, M. A. LOCK, S. RUNDLE, AND B. J. PETERSON. 1988. Nutrient influence on a stream grazer: *Orthocladius* microcommunities respond to nutrient input. Ecology 69:1383–1392.

HILL, W. R. AND A. W. KNIGHT. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955–1965.

———. 1988. Concurrent grazing effects of two stream insects on periphyton. Limnol. Oceanogr. 33:15–26.

JACOBY, J. M. 1985. Grazing effects on periphyton by *Theodoxus fluviatilis* (Gastropoda) in a lowland stream. J. Freshw. Ecol. 3:265–274.

KEHDE, P. M. AND J. L. WILHM. 1972. The effects of grazing by snails on community structure of periphyton in laboratory streams. Am. Midl. Nat. 87:8–24.

LAMBERTI, G. A. AND V. H. RESH. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124–1135.

LAMBERTI, G. A., L. R. ASHKENAS, S. V. GREGORY, AND A. D. STEINMAN. 1987a. Effects of three herbivores on periphyton communities in laboratory streams. J. N. Am. Benthol. Soc. 6:92–104.

LAMBERTI, G. A., J. W. FEMINELLA, AND V. H. RESH. 1987b. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia 73:75–81.

MOORE, J. W. 1975. The role of algae in the diet of *Asellus aquaticus* and *Gammarus pulex*. J. Animal Ecol. 4:719–730.

———. 1977a. Some aspects of the feeding biology of benthic herbivores. Hydrobiologia 53:139–146.

———. 1977b. Some factors affecting algal consumption in subarctic Ephemeroptera, Plecoptera, and Simuliidae. Oecologia 27:261–273.

OEMKE, M. P. 1984. Diatom feeding preferences of *Glossosoma nigrior* (Banks) larvae in two southern Michigan streams. Pp. 265–290 *in* Fourth International Symposium on Trichoptera, J. C. Morse ed. W. Junk, The Hague.

OEMKE, M. P. AND T. M. BURTON. 1986. Diatom colonization dynamics in a lotic system. Hydrobiologia 139:153–166.

PATRICK, R. 1970. Benthic stream communities. Am. Sci. 58:546–549.

PETERSON, C. T. 1987. Gut passage and insect grazer selectivity of lotic diatoms. Freshw. Biol. 18:455–460.

POWER M. E., A. J. STEWART, AND W. J. MATTHEWS. 1988. Grazer control of algae in an Ozark Mountain stream. Effects of short term exclusion. Ecology 69:1894–1898.

STEINMAN, A. D., C. D. MCINTIRE, S. V. GREGORY, G. A. LAMBERTI, AND L. R. ASHKENAS. 1987. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. J. N. Am. Benthol. Soc. 6:175–188.

SUMNER, W. T. AND C. D. MCINTIRE. 1982. Grazer-periphyton interactions in laboratory streams. Arch. Hydrobiol. 93:135– 157.

Effects of Stream Order and Alkalinity on The Composition of Diatom Communities in Two Northern Michigan River Systems

by

Thomas M. Burton

Departments of Zoology and Fisheries and Wildlife,
Michigan State University, East Lansing, Michigan 48824

and

Mark P. Oemke and Jennifer M. Molloy

Department of Zoology, Michigan State University,
East Lansing, Michigan 48824

with 1 figure and 3 tables

Abstract: The composition of benthic diatom communities was determined from four sites representing first, second, third, and fourth order streams in two river systems in northern Michigan in August, 1987. One of these river systems was a low-alkalinity system (10–12 mg $CaCO_3$/L) and the other was a high-alkalinity system (137–182 mg $CaCO_3$/L) despite occupying contiguous drainage basins. There was no consistent increase with stream order as is implied by the River Continuum Concept in either diatom cell density or in chlorophyll *a* concentrations from the streams. Substrates from the high-alkalinity river sites had higher diatom densities (2543–7079 cells mm^{-2}) and larger standing crops of chlorophyll a (5.1–13.7 mg m^{-2}) than did those from the low-alkalinity rivers (223–909 cells mm^{-2} and 0.2–1.1 mg Chl. *a* m^{-2} respectively). The higher diatom densities and chlorophyll levels in the high-alkalinity system occurred in the river system with the lowest N and P levels in stream water. There was a shift in diatom community composition in a downstream direction in the low-alkalinity system with the first order system nearly equally dominated by *Eunotia curvata, E. pectinalis, Fragilaria atomus, Tabellaria fenestrata,* and *T. flocculosa*. Dominance strongly shifted towards *F. atomus* at the second order site and to a combination of *E. pectinalis* and *Achnanthes linearis* at the third and fourth order sites. The high-alkalinity system was characterized by fewer taxa per site, and dominance did not shift much in a downstream direction. *Cocconeis placentula* var. *placentula* achieved very high dominance in the first, second, and third order streams with *C. placentula* var. *lineata* comprising most of the reminder of the community. For the fourth order, high-alkalinity site, *C. placentula* var. *lineata* became more dominant than *C. placentula* var. *placentula*, and *Achnanthes minutissima* achieved a level of greater than 5 % dominance for the first time.

TABLE 1. Chemical and physical data* (mean ± S.E.) for the Peshekee and Ford rivers.

	Ford River system				Peshekee river system			
Stream order	1	2	3	4	1	2	3	4
ph	7.9 ± 0.1	7.9 ± 0.1	8.0 ± 0.1	7.9 ± 0.04	6.1 ± 0.2	5.9 ± 0.1	6.1 ± 0.2	6.6 ± 0.1
Alkalinity	182 ± 4	162 ± 12	137 ± 6	144 ± 11	11 ± 1	10 ± 1	12 ± 2	12 ± 2
Dissolved oxygen	9.7 ± 0.3	8.8 ± 0.8	9.1 ± 0.3	8.4 ± 0.2	5.7 ± 0.4	4.4 ± 0.4	5.4 ± 0.7	8.2 ± 0.4
Conductance	269 ± 16	232 ± 22	199 ± 23	241 ± 11	18 ± 2	21 ± 2	24 ± 1	25 ± 1
Silicate - Si	12 ± 0.1	11 ± 0.3	10 ± 0.4	9 ± 0.3	4 ± 0.2	5 ± 0.3	5 ± 0.1	6 ± 0.3
Ammonium -N	17 ± 2	31 ± 4	20 ± 0	22 ± 1	47 ± 3	47 ± 1	48 ± 2	44 ± 2
Nitrate - N	15 ± 1	19 ± 1	31 ± 5	10 ± 1	18 ± 1	18 ± 1	21 ± 3	29 ± 2
Inorganic - N	37 ± 2	56 ± 4	56 ± 5	34 ± 3	68 ± 3	70 ± 1	73 ± 3	78 ± 4
Organic - N	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.2	1.5 ± 0.1	1.2 ± 0.1	1.2 ± 0.2	1.4 ± 0.1	1.2 ± 0.1
Soluble reactive P	4 ± 2	8 ± 2	6 ± 2	4 ± 1	17 ± 2	19 ± 4	18 ± 3	21 ± 4
Total P	10 ± 0	11 ± 1	12 ± 2	32 ± 3	24 ± 2	23 ± 2	24 ± 3	23 ± 2
Temperature	12 ± 1	14 ± 1	16 ± 1	17 ± 1	15 ± 1	15 ± 2	16 ± 2	16 ± 2
Width (m)	0.5 – 1.1	2.3 – 6.0	6 – 8	10 – 12	1.2 – 2.1	2.9 – 4.5	4 – 6	9 – 12
Depth (cm)	9 – 18	20 – 39	31 – 37	17 – 34	17 – 30	11 – 35	10 – 36	15 – 72
Velocity (cm/sec)	15 – 38	17 – 41	30 – 75	57 – 74	13 – 59	20 – 61	15 – 54	45 – 75

*Units of measure: pH = pH units; Alkalinity = mg $CaCO_3$/L; Dissolved oxygen = mg O_2/L; Specific conductance = µmhos; Silicate - Si, Ammonium - N, Nitrate - N, Inorganic - N, Soluble reactive P, and Total P are in µg/L; Organic - N = mg/L; Temperature = degrees C; Width = range of width of stream (m) within 10 m of substrate placement; Depth = range of depth of exposure of substrates beneath the water surface in cm; Velocity = cm/sec.

Introduction

According to the river continuum concept (Minshall et al. 1985; Vannote et al. 1980), benthic diatom production is low in headwater streams because of shading and increases in a downstream direction until turbidity and depth limits production. Changes in diatom community structure are to be expected along this continuum but have received only limited attention.

Lay and Ward (1987) demonstrated that geology was important in determining diatom community structure in the southeastern United States, particularly through its impact on alkalinity and nutrient availability (also see Meyer et al. 1988). No study, to our knowledge, has examined the impact of alkalinity on diatom community structure along the stream continuum. Our objective in this study was to provide comparative data on changes in diatom community structure along the river continuum for two contiguous fourth order river systems in northern Michigan with one river having low alkalinity and the other high alkalinity (Table 1).

Materials and Methods

The diatom communities were sampled in erosional zones at a first, second, third, and fourth order site in each of the river systems for a 28-day period in August 1987 using standard 7.6×2.5 cm glass microscope slides as artificial substrates. Details of depth, width, and velocity of stream reaches at the point of substrate exposure are given in Table 1. A 28-day colonization period for microscope slides was selected based on previous studies of colonization dynamics in the Ford River, the high-alkalinity system used in this study (Oemke and Burton 1986). Oemke and Burton (1986, unpublished data) also compared diatom communities on microscope slides and natural rock surfaces in the river and established that diatom community composition on the microscope slides were qualitatively similar to community composition on nearby rock surfaces.

Sampling, slide preparation, counting, and calculation procedures followed those detailed by Oemke and Burton (1986). Six slides were air-dried at the end of the study period for species composition and cell count determination, and 10 slides were frozen for chlorophyll a analysis following the fluorometric procedure in Standard Methods (American Public Health Association 1985).

The two rivers selected for study were located in the Lake Michigan drainage of the western upper peninsula of Michigan. The study sites in the Ford River system (high alkalinity, see Table 1) were all located in northern Dickinson County. The first order site (Sec. 18, T. 44 N., R. 29 W.) was a small unnamed, heavily shaded tributary that drained through a cedar (*Thuja occidentalis*) swamp with an understory of speckled alder (*Alnus rugosa*) into the upper portion of Two Mile Creek. The sampling point was about 100 m from the confluence of the first order stream with Two Mile Creek. The second order site was located on Two Mile Creek (Sec. 19, T. 44 N., R. 29 W.) about 300 m downstream of its confluence with the small first order stream used as the first order site. The second order stream site was also heavily shaded by riparian vegetation dominated by cedar and speckled alder. The third order site was located on Two Mile Creek just upstream of its confluence with the Ford River (Sec. 18, T. 43 N., R. 29 W.). The mid-channel placement of the substrates resulted in exposure to sunlight during midday, but these substrates were shaded during most of the day by riparian vegetation dominated by balsam poplar (*Populus balsamifera*) and speckled alder. The fourth order site was on the Ford River (Sec. 21, T. 43 N., R. 28 W.). Placement of the substrates at this site was at a point in the river that received sunlight for several hours per day with early morning and late afternoon shading by riparian vegetation dominated by balsam poplar and speckled

TABLE 2. Biological characterization of the low-alkalinity Peshekee and high-alkalinity Ford river systems by stream orders sampled. Values are means ± S.E., N = 6 unless otherwise indicated.

	Stream Order			
	1st Order	2nd Order	3rd Order	4th Order
Peshekee chl. *a* ($mg \cdot m^{-2}$)	0.42 ± 0.05	0.17 ± 0.03	0.9 ± 0.10	1.11 ± 0.15
Ford chl. *a* ($mg \cdot m^{-2}$)	5.10 ± 0.72	12.88 ± 0.98	13.66 ± 0.56	9.85 ± 0.81
Peshekee density ($cells \cdot mm^{-2}$)	223 ± 19	859 ± 169	567 ± 113	909 ± 83
Ford density ($cells \cdot mm^{-2}$)	3779 ± 256	7079 ± 1145	6032 ± 810	2543 ± 246*
Peshekee diversity (H′)	2.62 ± 0.06	1.79 ± 0.12	1.81 ± 0.18	1.66 ± 0.13
Ford diversity (H′)	0.70 ± 0.10	0.96 ± 0.01	0.59 ± 0.04*	2.42 ± 0.16*
Peshekee evenness (J′)	0.93 ± 0.01	0.72 ± 0.04	0.77 ± 0.05	0.75 ± 0.04
Ford evenness (J′)	0.36 ± 0.06	0.54 ± 0.04	0.32 ± 0.02	0.70 ± 0.01*
Peshekee taxa /slide	23.8 ± 1.25	17.0 ± 1.21	15.0 ± 1.55	13.2 ± 1.05
Ford taxa/slide	7.83 ± 0.87	9.17 ± 1.30	7.17 ± 1.14	32.33 ± 5.90*
Peshekee total taxa	42	33	33	27
Ford total taxa	17	24	16	53*

*N = 10 for all chlorophyll *a* determinations except Peshekee 4th order site where N = 7; N = 3 for Ford River 4th order site for count-based statistics, and they were done by a different observer (MO instead of JM).

alder. See Table 1 for details of chemistry, depth of substrate placement, width of the stream, and current velocities for these sites.

The Peshekee River (low alkalinity, see Table 1) was much blacker in color than the brown water Ford River, which suggested greater inputs of organic acids. No analysis of land use for the basin was done, but speckled alder swamps and sedge meadows appeared to be much more common for this catchment than for the Ford River catchment. The most common vegetation type in the catchments of both basins appeared to be early successional northern hardwoods forests dominated by quaking aspen, *Populus tremuloides*. However, a greater percentage of the area appeared to be in conifers in the Peshekee River catchment. The darker color of this river may be related to the apparent greater percentage of watershed area in wetlands and coniferous forests.

The first order site on the Peshekee River was located in Baraga County (Sec. 21, T. 50 N., R. 31 W.) in a heavily shaded area of riparian vegetation dominated by *Populus tremuloides* but just downstream of an extensive speckled alder (*Alnus rugosa*) swamp. The heavily shaded second order site (Sec. 36, T. 50 N., R. 31 W. in Baraga County) was a tributary to the Peshekee River that drained a speckled alder swamp, and thick high shrubs of speckled alder formed a complete canopy over the stream. The third order site was on the Peshekee River (Sec. 27, T. 50 N., R. 31 W. in Baraga County) upstream of its confluence with the second order site. The placement of the substrates in midstream at this site resulted in some exposure to sunlight during midday, but shading was provided for most of the day by speckled alders along the bank. This site was in the middle of an extensive area of sedge meadow wetland. The placement of substrates in the Peshekee River at the fourth order site (Sec. 1, T. 48 N., R. 30 W. in Marquette County) resulted

in exposure to sunlight during most of the day, but early morning and late afternoon shading was provided by the mixed spruce-hardwoods forest and by clumps of speckled alder along the bank. See Table 1 for details of chemistry, depth of substrate placement, width of the stream, and current velocities for these sites.

Water samples were taken during initial placement of the artificial substrates and once per week thereafter (N = 5) at each site over the 28-day period. Nutrient analyses (N, P, Si) were conducted using autoanalyzer techniques recommended by the U. S. Environmental Protection Agency (U. S. Environmental Protection Agency 1979) or procedures in Standard Methods (American Public Health Association 1985).

Results

Changes in diatom density and chlorophyll a did not increase consistently with stream order in the low-alkalinity Peshekee or the high-alkalinity Ford Rivers (Table 2). Diatom density increased 3.9 fold from the first to the second order sites in the low-alkalinity Peshekee River but then decreased slightly at the third order site before reaching a peak at the fourth order site (Table 2).

There was an increase of 1.9 fold in cell density from the first order to the second order site in the Ford River with a slight decrease from the second to the third order site followed by a decrease at the fourth order site (Table 2). The fourth order site was characterized by lower cell density than was the first order site. Chlorophyll a concentrations followed a different pattern with the highest value occurring at the third order site followed by the second, fourth, and first order sites (Table 2).

Both cell density and chlorophyll a concentrations were consistently higher in the high-alkalinity Ford system than in the low-alkalinity Peshekee system (Table 2) despite higher values for inorganic nitrogen and soluble reactive and total phosphorus in the Peshekee River (Table 1).

Increase in cell density from the first to the second order stream in the Peshekee River system was accompanied by a decrease in diversity and evenness (Table 2) and a shift in species composition for the diatom community (Fig. 1A). At the first order site, dominance of the community was more equally distributed among species that achieved a level of 5 % or more of the counts than at any other site (Fig. 1A), and this shared dominance was reflected in the relatively high values for H' and evenness (Table 2). The 42 taxa (mean of 23.8 ± 1.3 (± S. E.) per slide) recorded from the slides at this site represented the highest species richness for any of the sites on the Peshekee or Ford rivers except for the Ford fourth order site (Table 2). *Eunotia pectinalis* (O. F. Müll.?) Rabh. var *pectinalis* was the most dominant member of the diatom community (17.9 % of total counts) followed by *Fragilaria atomus* var. *atomus* (13.4 %), *E. curvata* (Kütz.) Lagerst. var. *curvata* (13 %), *Tabellaria flocculosa* (Roth) Kütz. var. *flocculosa* (9.9 %), and *T. fenestrata* (Lyngb.) Kütz. var. *fenestrata* (6.3 %) (Fig. 1A).

At the second order site, dominance shifted strongly towards *Fragilaria atomus* var. *atomus* with this species comprising 53.4 % of the individuals in the community (Fig. 1A). *Tabellaria flocculosa* var. *flocculosa* (9.6 %) was the only other species to achieve greater than 3 % dominance at this site. The shift to greater dominance by *F. atomus* was accompanied by decreased values for diversity and evenness (Table 2), a drop in the total number of taxa identified from this second order site to 33 from the 42 identified at the first order site, and a drop in the average number of taxa per slide (Table 2).

At the third and fourth order sites in the Peshekee River, dominance shifted strongly to *Achnanthes linearis* (W. Sm.) Grun. var. *linearis* (44.5 and 45 % dominance respectively, Figure 1A).

Eunotia pectinalis var. *pectinalis* was the next most dominant member of the community at the third and fourth order sites (14.6 and 23.1 % dominance respectively, Figure 1A). *Fragilaria atomus* remained a dominant member of the community at the third order site (11.7 % of counts), but comprised only 3.6 % of the counts at the fourth order site (Figure 1A). *Fragilaria vaucheriae* (Kütz.) Peters. var. *vaucheriae* (6.4 %) and *Achnanthes minutissima* Kütz. var. *minutissima* (5.8 %) achieved greater than 5 % dominance for the first time along the river continuum at the fourth order site (Figure 1A). The total number of taxa identified from the third order sites was 33, as it had been at the second order site, but the average number of taxa per slide dropped slightly (Table 2). Diversity and evenness were similar for these two sites (Table 2). The total number of taxa collected, the average number of taxa per slide, diversity, and evenness all decreased slightly at the fourth order site compared to the third order site (Table 2).

Shifts in dominance from site to site recorded for the Peshekee River did not occur in the Ford River (Fig. 1B). The dominant species for all sites on the Ford River was *Cocconeis placentula* (Fig. 1B) with shifts occurring primarily at the variety level. *Cocconeis placentula* Ehrenberg var. *placentula* dominated community structure in the first, second, and third order streams, while *C. placentula* var. *lineata* (Ehrenberg) V. H. dominated community structure in the fourth order stream (Fig. 1B). *Achnanthes minutissima* var. *minutissima* was the only other species to achieve greater than 5 % dominance of total individuals present, and only at the fourth order site (8.9 ± 1.4 % (mean ± S. E.) of total counts) (Fig. 1B).

Diversity and evenness were greatest for the fourth order stream diatom community for the Ford River system in contrast to the situation in the Peshekee River system (Table 2). Diversity and evenness were also substantially lower in the Ford River system at all sites than they were in the Peshekee River system (Table 2), and fewer taxa were present except at the fourth order site (Table 2). There is a possibility of observer bias at the Ford fourth order site, since these samples were counted by MO instead of JM. However, counts by JM of control substrates of 10 m mesh nylon netting in a related study at this site (Burton et al. 1990) resulted in average taxa estimates of 16.3 ± 1.7 (mean ± S.E.), total taxa estimates of 20 (see Table 3 for list), diversity estimates of 1.5 ± 0.1, evenness estimates of 0.73 ± 0.02, and density estimates of 2269 ± 1246 cells mm^{-2}. Even these lower estimates indicate that the increases in diversity, evenness, and decrease in cell density are real for this site.

The only genus that occurred as a dominant in the low-alkalinity Peshekee but was never collected from the high-alkalinity Ford River system was *Tabellaria* (Figure 1). Although never achieving more than 5 % dominance, *Frustulia vulgaris* (Thwaites) DeT. also occurred commonly in the Peshekee and was never collected from the Ford River system (Table 3). Several species and varieties of *Eunotia* (*E. curvata*, *E. diodon*, *E. pectinalis* var. *minor*, *E. serra*, *E. tenella*, *E. triodon*), *Fragilaria* (*F. crotonensis*, *F. virescens*), *Gomphonema* (*G. acuminatum*, *G. constrictum*, *G. helvetica*, *G. sphaerophorum*), and *Navicula* (*N. mutica*, *N. oblonga*, *N. symmetrica*, *N. viridula*) occurred in the low-alkalinity Peshekee but were never collected from the high-alkalinity Ford, although at least one species of each genus occurred in both rivers (Table 3). Two *Eunotia* species occurred as dominant members of the community in the low-alkalinity Peshekee (Figure 1), while *E. pectinalis* var. *pectinalis*, an uncommon member of the first and second order stream diatom communities, was the only member of the genus that occurred in the high-alkalinity

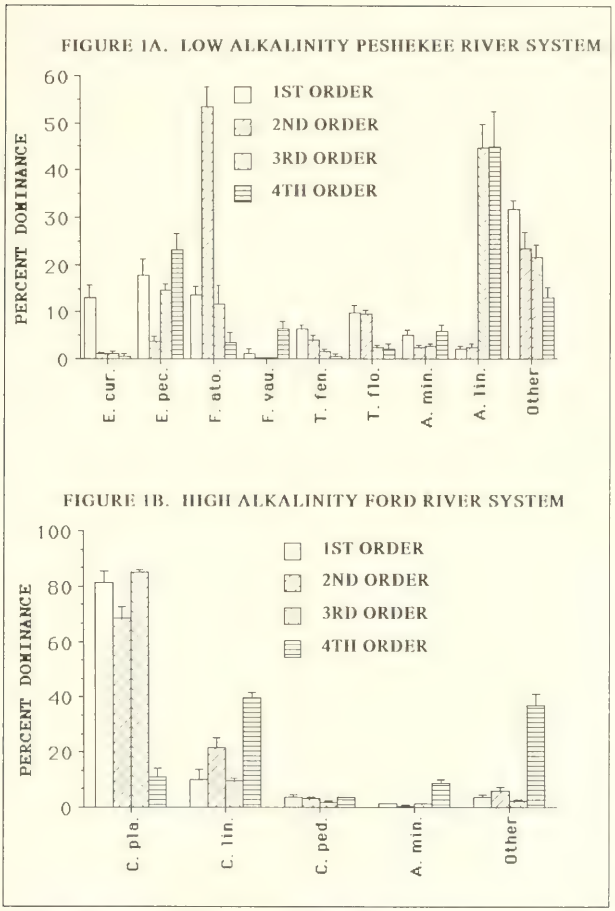


FIGURE 1A. Percent dominance for the species of diatoms that achieved greater than 5 % dominance of total counts at any of the sites in the low-alkalinity Peshekee River. E. cur. = *Eunotia curvata* var. *curvata*, E. pec. = *Eunotia pectinalis* var. *pectinalis*; F. ato. = *Fragilaria atomus* var. *atomus*; F. vau. = *Fragilaria vaucheriae* var. *vaucheriae*; T. fen. = *Tabellaria fenestrata* var. *fenestrata*; T. flo. = *Tabellaria flocculosa* var. *flocculosa*; A. min. = *Achnanthes minutissima* var. *minutissima*; A. lin. = *Achnanthes linearis* var. *linearis*; Other = sum of all other species. Error bars = one standard error. FIGURE 1B. Percent dominance for the species of diatoms that achieved greater than 5 % of total counts at any of the sites in the high-alkalinity Ford River. C. pla. = *Cocconeis placentula* var. *placentula*; C. lin. = *Cocconeis placentula* var. *lineata*; C. ped. = *Cocconeis pediculus* var. *pediculus*; A. min. = *Achnanthes minutissima* var. *minutissima*; Other = sum of all other species. Error bars = one standard error.

Ford River (Table 3). The reverse situation occurred with the three *Cocconeis* taxa, since they dominated the counts in the high-alkalinity Ford system (Fig. 1) but occurred only rarely in the first to third order streams of the Peshekee system (Table 3). The most common taxa (1.9–2.6 % dominance) in the Ford River system other than those reported in Figure 1 were *Achnanthes stewartii*, *Cyclotella meneghiniana*, *Fragilaria construens*, *F. vaucheriae*, and *Navicula salinarum* (Table 3). All of these taxa except *F. construens* were also found in the Peshekee River system.

Discussion

The river continuum concept (Vannote et al. 1980) suggests that primary production and diversity should increase along the river continuum from first order stream through middle-sized sixth or seventh order rivers. The increase in production implies an increase in both cell number and chlorophyll a production along the continuum. Our data do not support a gradual increase in these parameters along a first to fourth order river continuum in either of the two northern Michigan rivers studied (Table 2).

It has been suggested that high-alkalinity streams support higher fish and invertebrate production than do low-alkalinity ones (Arnold et al. 1981; Egglishaw 1968; Krueger and Waters 1983; Tarzwell 1938). One explanation for these observations is that low-alkalinity streams support lower primary production and provide less food for fish and invertebrates than do high-alkalinity streams. If primary productivity is lower, then cell counts and chlorophyll a production should also be lower in low-alkalinity systems unless turnover rate is very slow due to low rates of gazing by invertebrates or fish or due to lower rates of senescence and decomposition in the low-alkalinity system. Our data support this idea since both cell counts and chlorophyll were significantly lower in the Peshekee River than in the Ford River with its higher alkalinity (Table 2).

Lay and Ward (1987) suggested that nutrient limitation might mask differences in primary production in low- and high-alkalinity systems. In our study, the high-alkalinity Ford River actually contained lower concentrations of both nitrogen and phosphorus than did the low-alkalinity Peshekee River system (Table 1). Despite higher nutrient levels, cell density and chlorophyll a levels were much lower in the Peshekee River system (Table 2). It seems unlikely that uptake of N and P by diatoms in either river would have been great enough to have substantially lowered nutrients in stream water given the oligotrophic status and modest amounts of chlorophyll of both rivers. In previous experiments, however, addition of N and P to these two river systems during low-flow conditions resulted in changes in community structure for both rivers with greatest changes occurring in the low-alkalinity, but more nutrient-rich Peshekee (Burton et al. 1991). Thus, a nutrient effect cannot be ruled out. Either the dominant diatom species in the low-alkalinity system require higher nutrient levels for growth or the apparently available nutrients in the Peshekee are unavailable because of chelation, sorption, or other interactions with the organic materials in this blackwater river.

Acknowledgements

Partial support for this research was provided by the U. S. Navy through a subcontract to Michigan State University under contract N00039-84-C-0070 to IIT Research Institute. We thank Natalie Breithaupt, Dennis Mullen, and Michael O'Malley for technical help and Delorus Burton for assistance in collection of field samples.

TABLE 3. Diatoms from the Peshekee and Ford rivers, August, 1987.

	Peshekee River				Ford River			
Stream Order	1	2	3	4	1	2	3	4
Achnanthes clevei Grun.			x	x			x	
Achnanthes clevei var. *rostrata* Hust.	x				x		x	
Achnanthes hauckiana Grun.						x		
Achnanthes lanceolata Breb. *ex* Kütz.				x		x		x
Achnanthes lanceolata var. *dubia* Grun.		x	x	x	x	x	x	
Achnanthes linearis (W. Sm.) Grun.	x	x	x	x		x	x	x
Achnanthes minutissima Kütz.	x	x	x	x	x	x	x	x
Achnanthes peragalli Brun. & Hérib.		x	x					
Achnanthes stewartii Patr.				x				
Amphipleura pellucida (Kütz.) Kütz.					x			x
Amphora ovalis (Kütz.) Kütz.	x			x		x		x
Amphora ovalis var. *pediculus* (Kütz.) V.H. *ex* DeT					x	x		
Amphora ovalis var. *perpusilla* (Grun.) Grun.								x
Cocconeis pediculus Ehr.	x				x	x	x	x
Cocconeis placentula Ehr.	x	x	x		x	x	x	
Cocconeis placentula var. *lineata* (Ehr.) V.H.	x	x	x		x	x	x	x
Cyclotella atomus Hust.	x	x	x			x	x	
Cyclotella meneghiniana Kütz.		x	x	x	x	x	x	x
Cymbella lunata W. Sm.	x		x					
Cymbella minuta Hilse *ex* Rabh.	x			x	x			x
Cymbella minuta var. *pseudogracilis* (Choln.) Reim..			x					
Diatoma hiemale (Roth) Heib.						x		
Diatoma tenue var. *elongatum* Lyngb.			x					
Epithemia sorex Kütz.						x		
Eunotia curvata (Kütz.) Lagerst.	x	x	x	x				
Eunotia diodon Ehr..	x	x						
Eunotia pectinalis (O.F. Mull.?) Rabh.	x	x	x	x	x	x		
Eunotia pectinalis var. *minor* (Kütz.) Rabh.	x	x	x	x				
Eunotia serra var. *diadema* (Ehr.) Patr.		x						
Eunotia tenella (Grun.) Cl.	x							
Eunotia triodon Ehr.				x				

TABLE 3, continued.

	Peshekee River				Ford River			
Stream Order	1	2	3	4	1	2	3	4
Fragilaria atomus Hust.	x	x	x	x				
Fragilaria crotonensis Kitton	x		x	x				
Fragilaria vaucheriae (Kütz.) Peters	x	x	x	x	x	x	x	x
Fragilaria virescens Ralfs.	x							
Frustulia vulgaris (Thwaites) DeT.	x	x	x	x				
Gomphonema acuminatum Ehr.		x	x					
Gomphonema constrictum Ehr.	x							
Gomphonema gracile Ehr.	x	x	x	x				
Gomphonema helveticum Brun.		x						
Gomphonema parvulum (Kütz.) Kütz.	x	x	x	x	x	x	x	x
Gomphonema sphaerophorum Ehr.	x							
Gomphonema Ehr. sp.					x			
Melosira granulata (Ehr.) Ralfs.	x	x	x	x				
Melosira varians Ag.					x			
Meridion circulare (Grev.) Ag.	x	x				x		
Navicula cryptocephala Kütz.	x							
Navicula cryptocephala var. *veneta* (Kütz.) Rabh.	x	x	x	x	x	x	x	x
Navicula mutica var. *cohnii* (Hilse) Grun.		x						
Navicula oblonga (Kütz.) Kütz.						x		
Navicula pupula Kütz			x					
Navicula pupula var. *capitata* Skv. & Meyer	x							
Navicula salinarum var. *intermedia* (Grun.) Cl.	x	x	x					x
Navicula symmetrica Patr.	x							
Navicula viridula (Kütz.) Kütz. emend. V.H.	x							
Nitzschia acicularis W. Sm.				x			x	
Nitzschia dissipata (Kütz.) Grun.	x							
Nitzschia frustulum var. *perpusilla* (Rabh.) Grun.	x		x			x		
Nitzschia linearis W. Sm.	x	x	x		x	x		
Nitzschia longissima (Bréb.) Ralfs.	x	x	x	x				
Nitzschia palea (Kütz.) W. Sm.	x	x	x					x
Nitzschia palea var. *debilis* (Kütz.) Grun.	x							

TABLE 3, continued.

	Peshekee River				Ford River			
Stream Order	1	2	3	4	1	2	3	4
Opephora martyi Hérib.		x						
Pinnularia hilseana Jan.	x	x		x				
Synedra delicatissima W. Sm.								x
Synedra parasitica (W.S.) Hust.							x	
Synedra ulna (Nitz.) Ehr.	x	x	x	x	x	x	x	x
Tabellaria fenestrata (Lyngb.) Kütz	x	x	x	x				
Tabellaria flocculosa (Roth) Kütz.	x	x	x	x				
Total taxa (unident. included)	42	33	33	27	17	24	16	20

Literature Cited

AMERICAN PUBLIC HEALTH ASSOCIATION. 1985. Standard Methods for the Examination of Water and Wastewater. Sixteenth Edition. American Public Health Association, Washington, D. C. 1268 pp.

ARNOLD, D. E., P. M. BENDER, A. B. HALE, AND R. W. LIGHT. 1981. Studies on infertile, acidic Pennsylvania streams and their benthic communities. Pp. 15–33 *in* Effects of Acidic Precipitation on Benthos, Proceedings of a Symposium, R. Singer, ed. North American Benthological Society.

BURTON, T. M., M. P. OEMKE, AND J. M. MOLLOY. 1991. Contrasting effects of nitrogen and phosphorus additions on epilithic algae in a hardwater and a softwater stream in northern Michigan. Verh. Int. Verein. Theor. Angew. Limnol. 24:1644–1653.

EGGLISHAW, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. J. Appl. Ecol. 5:731–740.

KRUEGER, C. C. AND T. R. WATERS. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64:840–850.

LAY, J. A. AND A. K. WARD. 1987. Algal community dynamics in two streams associated with different geological regions in the southeastern United States. Arch. Hydrobiol. 108:305–324.

MEYER, J. L., W. H. MCDOWELL, T. L. BOTT, J. W. ELWOOD, C. ISHIZAKI, J. M. MELACK, B. L. PECKARSKY, B. J. PETERSON, AND P. A. RUBLEE. 1988. Elemental dynamics in streams. J. N. Am. Benthol. Soc. 7:410–432.

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSON, C. E. CUSHING, D. A. BRUNS, J. R. SEDELL, AND R. L. VANNOTE. 1985. Developments in stream ecosystem theory. Can J. Fish. Aq. Sci. 42:1045–1055.

OEMKE, M. P. AND T. M. BURTON. 1986. Diatom colonization dynamics in a lotic system. Hydrobiologia 139:153–166.

TARZWELL, C. M. 1938. Factors influencing fish food and fish production in southwestern streams. Trans. Am. Fish. Soc. 67:246–255.

United States Environmental Protection Agency. 1979. Methods for Chemical Analysis of Water and Wastes. EPA-600/479-020, U. S. Environmental Protection Agency, Cincinnati, Ohio.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aq. Sci. 37:130–137.

Seasonal, Interannual, and Long-term Dynamics of Planktonic Diatoms in Oligotrophic Lake Tahoe

by

Heath J. Carney, Deborah A. Hunter, and Charles R. Goldman

Institute of Ecology and Division of Environmental Studies,
University of California, Davis, California 95616

with 2 figures

Abstract: Lake Tahoe is an ideal system for the study of diatom dynamics across temporal scales. They (and closely related chrysophytes) are abundant and remain dominant seasonally through the summer. Plankton samples have been collected for several decades, and diatoms are also well preserved in the sediments. Thus, diatom dynamics are examined here at three temporal scales: seasonality, interannual variability, and long-term trends. Seasonal succession rates are relatively low, and several reasons are provided for this. Dominant species are regulated primarily by nutrient- and light-limited growth, natural death, and sinking. Interannual variability seems quite substantial, since the dominant species change from one year to the next. This variability may be due largely to the inconsistent mixing depth during spring. The extent of mixing determines the nutrient and phytoplankton "seed" populations available for the spring/summer growth period. Intermediate time scales need much more additional study in relation to the other scales. Long-term data (neolimnological + paleolimnological) demonstrate a "signal" of gradual eutrophication superimposed above the "noise" of interannual variability. Since Lake Tahoe is still relatively oligotrophic, it serves as a present-day analog for the condition of lakes in other regions before human disturbance. As such, it is useful in comparative studies of diatom dynamics and human impacts.

Introduction

The potential insight gained from studying population and community dynamics across a range of temporal and spatial scales is clear (Frost et al. 1988; Likens 1989; Powell 1989; Magnuson 1990). Long-term data (at the scale of decades) indicate patterns and causal factors that are most important over time, while mechanisms giving rise to long-term trends operate at the seasonal time scale. Interannual dynamics are a critical link in that they provide comparisons for different seasons and comprise the variability against which long-term trends must be compared. Thus, studies at these time scales are complementary to one another rather than distinct alternatives. Nevertheless, few studies address this coupling, so the interaction between time scales remains poorly understood. Diatoms are particularly useful study organisms since their distinct and durable frustules can be analyzed for a great variety of samples (e.g., live, prepared plankton slides, sediment slides, etc). Despite this, the vast majority of diatom work is at a given time scale for

one or more systems rather than across time scales for a given system. One notable exception is a comparison by Haworth (1980) of long-term, weekly phytoplankton counts (1945–1977) to core profiles in Blelham Tarn of the English Lake District. However, even in this case, a posteriori comparisons of the sediment core patterns were made with previous phytoplankton counts of J. W. Lund.

Diatom studies in the Sierra Nevada, California, are quite important and promising in this respect, for a number of reasons. Lakes in this region are largely unexplored relative to the eastern United States and Europe, and they are quite distinct. Most are located in granitic basins with poorly developed soils (Melack et al. 1987; Goldman 1988; Whiting et al. 1989). Thus, both stream and lake water are quite low in nutrients, which is favorable for diatoms and chrysophytes. This sensitive region is now subject to unprecedented human pressures. While there has been human activity in the region for several centuries, the really substantial increase in human settlement in areas such as the Tahoe basin have occurred within recent decades (Goldman 1988).

Lake Tahoe is particularly appropriate for an analysis of diatom dynamics across temporal scales because it has been the subject of a long-term monitoring study and other investigations since 1959. We review and synthesize here data at the seasonal, interannual, and long-term (several decades) scales. Lake Tahoe is in some ways unusual because it is the largest among Sierra Nevada lakes (156 km^3). However, like other lakes in this region it is oligotrophic, dominated by diatoms and chrysophytes, and responding to human pressures. We clarify similarities and differences to other systems where appropriate.

Results and Discussion

Through the years Lake Tahoe phytoplankton has been studied by different investigators with somewhat different methodologies. Still, there is a consensus that diatoms have always been abundant and diverse. During 1967–1971 Anne Sands identified over 160 phytoplankton species, of which 112 were diatoms (10 centrics, the rest pennates; Goldman 1974). The five most dominant species in cell numbers were diatoms: *Fragilaria crotonensis* Kitton, *Melosira italica* (Ehrenberg) Kützing, *F. pinnata* Ehrenberg, *Stephanodiscus alpinus* Hustedt, and *Cyclotella bodanica* Eulenstein. These are relatively large-celled species, so they were also biomass dominants. For 1982–1987 Hunter et al. (1990) show that diatoms are the most abundant algal group according to biomass, especially during the spring and summer, and that chrysophytes and cryptophytes are also important. Diatoms generally comprise over 40 % of the total biomass, while the three groups together almost always account for over 80 % of the total biomass. Byron and Eloranta (1984) found 190 diatom species, including 164 littoral forms, in sediment samples. Here we review the most relevant studies for three time scales.

Seasonality

Species-level information on full annual cycles for diatoms and other phytoplankton is primarily from the above-mentioned counts of 1967–71 and 1982–87. Goldman (1974) presents data for 13 dominant species; plots for five diatoms during 1967–71 are shown in Figure 1. What is most striking for all these species is the lack of a clear and repeatable seasonal trend. Part of the reason may be that both live and dead cells were counted, and average concentrations in the top 105 m are plotted. Thus dead and sinking diatoms are included in the plots, which obscures seasonal cycles of growth and reproduction. Hunter et al. (1990) distinguished live and dead cells during 1982–87 and their plot of live biomass does reveal marked peaks during spring and early summer. This is consistent with Carney et al.'s (1988) finding that the proportion of live and dividing diatom cells

was greatest during the spring season, while the proportion of empty frustules was greatest during late summer and fall. Thus some seasonality in diatom growth and abundance is evident, but it is still much less marked than in more eutrophic lakes where spring diatom blooms are short-lived and may be replaced entirely by groups such as filamentous greens and blue-greens during summertime (Sommer et al. 1986).

Detailed measurements of diatom population processes and experiments on species interactions were completed during the mid-1980s (Carney 1987; Carney et al. 1988). Emphasis was placed on major processes affecting changes in concentrations of species in the water column. Terms in the following equation were measured in the field:

$$dN/dt = D + N[u-(s+ g+ d)]+ E,$$

where dN/dt was the net change in population per unit of time, D was the change in cell concentration due to turbulent diffusion, u was growth (cell division), s was sinking, g was grazing, d was death, and E was a residual term. Values for all these processes were converted to units of natural log per day (Guillard 1973). Diffusion, sinking, grazing, and death were referred to collectively as losses because all these processes had negative values where they were analyzed for dominant species. During spring and summer stratification growth was found to be the most important of these factors. Experimental bioassays determined that growth was limited by nutrients in the epilimnion (0–20 m) and by light at greater depths. It is important to note the recent shift from nitrogen to phosphorus limitation (Carney et al. 1988; Goldman 1988; Hunter et al. 1990). Light limitation in Lake Tahoe is also quite significant since the zone of mixing (epilimnion) is much shallower than the euphotic zone (1 % surface light level is up to 80–90 m). Thus, during summer stratification a relatively stable vertical gradient is established along which diatom species have been found to compete and segregate according to their resource-limited growth abilities (Carney 1987; Carney et al. 1988). By contrast, there is presently no evidence that these species segregate temporally by peaking at different times of the year. During 1985 the dominant *Cyclotella* and *Synedra* species all reached maximum abundance in late June and July (Carney et al. 1988:670). Thus, during the stratification period, the vertical spatial gradient seems to be relatively stable and of greater consequence to diatom species interactions than temporal gradients. In the oceans there may be even less seasonal succession in relation to the marked vertical gradients (Venrick 1990), so in this sense, Lake Tahoe may be part of a continuum between the oceans and small freshwater systems.

Sinking and natural death were the most important diatom losses during stratification of 1985. This was logically due to declining turbulence and nutrient depletion, and these processes led to the summertime collapse of the diatom populations. Both vertical diffusion and grazing were found to be relatively unimportant. The lack of grazing impact is noteworthy since it contrasts with so many other lakes. Two calanoid copepods, *Diaptomus tyrrelli* and *Epischura nevadensis*, have long dominated the zooplankton. Their low ambient concentrations and per capita filtering rates both contribute to their relatively insignificant grazing impact (Folt and Goldman 1981; Byron et al. 1984; Carney et al. 1988). Lake Tahoe appears to be at one end of a unimodal spectrum in which zooplankton grazing is relatively unimportant in very oligotrophic and eutrophic lakes, but quite important in mesotrophic systems (Carney and Elser 1990). *Daphnia* species may have had some impact in the past (Goldman 1974), and so may have greater grazing effects in the future. Recent small-scale introductions of *D. schodleri* in experimental enclosures have indicated that cladocerans can have a very substantial grazing impact (Elser et al. 1990). However, to observe such effects in the lake may require very substantial changes in the trophic state and plankton composition.

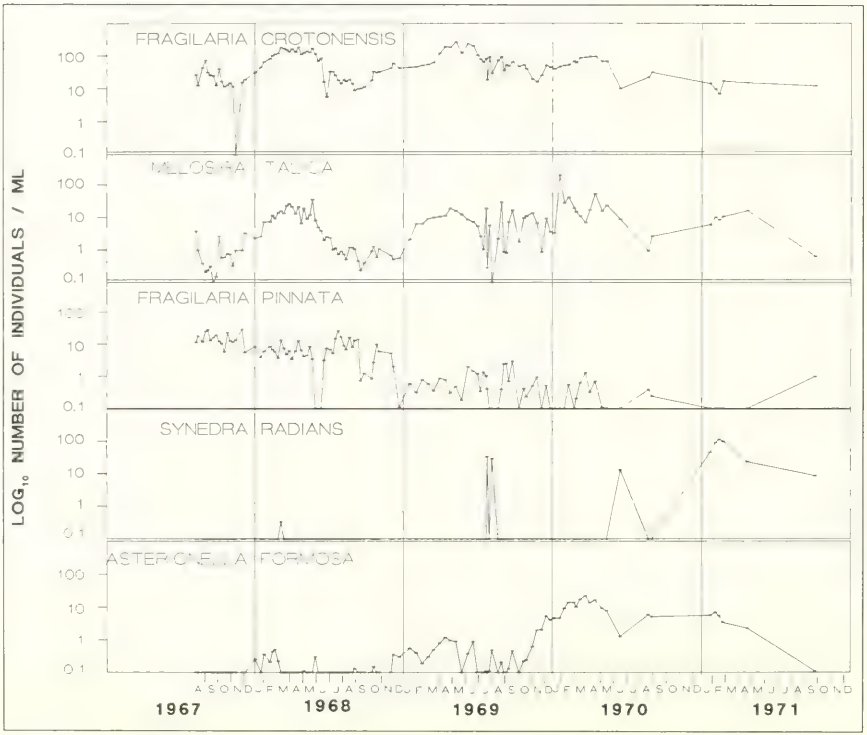

FRAGILARIA CROTONENSIS
MELOSIRA ITALICA
FRAGILARIA PINNATA
SYNEDRA RADIANS
ASTERIONELLA FORMOSA
100
10
1
0.1
LOG10 NUMBER OF INDIVIDUALS / ML
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1967
1968
1969
1970
1971

FIGURE 1. Abundances of five selected dominant diatoms at the index station of Lake Tahoe from mid-1967 through 1971 (modified from Goldman 1974).

The above studies give the qualitative impression that the seasonal succession of Lake Tahoe diatoms is relatively muted, driven and constrained primarily by physical and chemical factors, and resource-based competition, rather than by strong food web interactions. Williams and Goldman (1975) make quantitative comparisons, with a succession rate index, that confirm this impression. The succession rate they calculate for Lake Tahoe is substantially lower than for smaller more eutrophic temperate lakes, and only slightly higher than for tropical Lake Victoria. Carney and Goldman (1988) discuss several reasons for this: (a) diatoms persist through the summer and are not completely replaced by other groups because available nitrogen and phosphorus concentrations are quite low. Thus, available silica, which diatoms need for frustules, is not depleted as in more eutrophic lakes (Schelske et al. 1986); (b) the euphotic zone (up to 90–100 m) and total water column (up to 505 m) are much deeper than virtually all other lakes. Thus, it takes diatoms and other algae much longer to sink out of these zones; (c) the low grazing pressure is insufficient to select for the late successional green and blue-green species that are typically found in more eutrophic systems. Despite this muted seasonal succession and species turnover, Carney and Goldman (1988) find evidence for a modest shift from r- to K-selection during the stratification cycle.

Interannual Variability

To date no studies have focused on interannual variability of Lake Tahoe diatoms or other phytoplankton species. However, Goldman et al. (1989) have recently analyzed such variability for primary productivity, depth of spring mixing, and meteorological factors using the long-term data set. They found that the depth of spring mixing is an excellent predictor of primary productivity for a given year. In contrast with Castle Lake, a smaller mesotrophic lake in northern California, interannual variability does not appear to be affected by El Nino/Southern Oscillation (ENSO) events. This may be because the depth of mixing at Lake Tahoe is most affected by local weather events during March, whereas ENSO episodes influence climate at time scales up to 6–9 months.

These analyses give important clues about possible causes of diatom interannual variability. The timing and extent of spring mixing are critical in setting the initial conditions of nutrients and phytoplankton for each annual stratification cycle. The depth of mixing determines the amount of nutrients replenished to surface waters. This has been demonstrated most clearly for nitrate (Paerl et al. 1975). Perhaps at least as important for phytoplankton dynamics, but presently unknown, are the "seed" populations also brought up with mixing. How important is the composition of the spring "seed" assemblage in determining the dominant taxa of the coming year? By comparison, how important are nutrient levels and ratios?

While these questions can only be answered by future analyses and field studies, we can gain some understanding of the nature and extent of diatom interannual variability from count data for 1967–71 and 1982–87. During 1967–71 variation between years for all species seems quite significant (Fig. 1). *Fragilaria crotonensis* and *Melosira italica* are relatively stable, though they both virtually disappear later during the 1970s. *Fragilaria pinnata* gradually declines, diminishing especially after 1969. At the same time, *Synedra radians* Kützing and *Asterionella formosa* Hassall increase abruptly in abundance. These changes may be the result of an unusual mixing event in 1969. The effects of such an event appear to last for more than one year. Hunter et al. (1990) do not present species-level information. However, substantial interannual variability is evident in a group-level plot of 1982–87. Both relative and absolute diatom biomass is much greater during 1984 and 1985 than during 1986 and 1987. During 1984 *A. formosa* accounted for over 70 % of the unusually high spring diatom biomass, but this species was relatively insignificant the

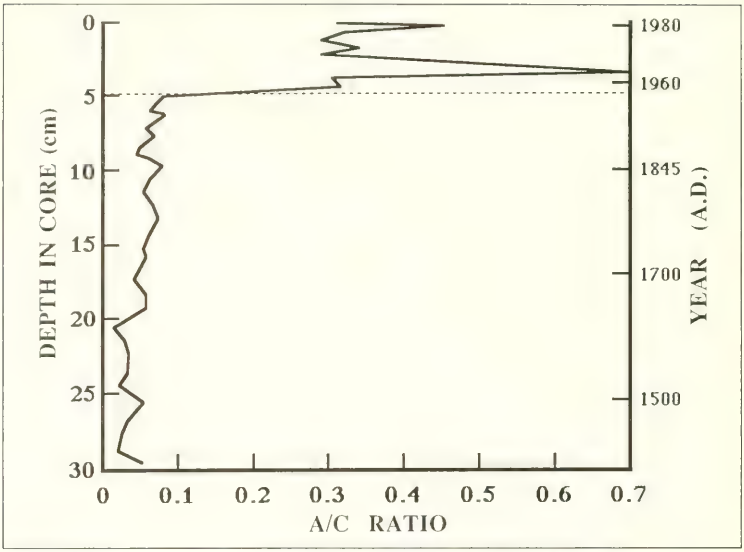


FIGURE 2. The ratio of araphid pennate to centric diatoms (A/C ratio) in a short midlake sediment core (modified from Byron and Eloranta 1984).

following year (D. Hunter, unpublished data). In 1986 and 1987 chrysophyte species, including *Uroglena americana* Calkins and *Dinobryon* spp. became relatively abundant during the summer.

LONG-TERM TRENDS

For the evaluation of long-term trends of planktonic diatoms at Lake Tahoe it is necessary to have continuous records for the duration of the monitoring program. Unfortunately, this information is not available. However, as for interannual variability, we can gain insights from the other types of data that have been collected and analyzed more continuously. There is substantial evidence for gradual eutrophication superimposed above the "noise" of interannual variability (Goldman 1988). Since 1959, primary productivity has increased an average of 5.6 %/yr. and the concomitant transparency decline has averaged 0.37 m/yr. Available nitrogen (as NO_3) in the water column has increased, while available phosphorus has not. Experimental bioassays indicate a recent shift from nitrogen to phosphorus limitation of phytoplankton growth (Goldman 1988; Carney et al. 1988). All these trends are consistent with the process of early eutrophication caused by human settlement and land use in the watershed.

The diatom data most comparable to these 30-year trends are counts from midlake sediment cores (Byron and Eloranta 1984). They find a substantial shift in diatom community composition associated with increasing human population (Fig. 2). During the late 1950s there is a substantial increase in the A/C (araphid pennate/centric) ratio, from < 0.1 to 0.7, due especially to the proportional increases of *Fragilaria crotonensis* and *Synedra*

species, and to declines in *Cyclotella ocellata* Pantocsek and *Melosira* species. Stockner (1972) proposed this ratio for indicating trophic state as follows: <1 oligotrophic, 1–2 mesotrophic, > 2 eutrophic. This ratio must be used with considerable caution; it is particularly misleading when eutrophic species of the genus *Stephanodiscus* occur (Brugam 1979; Carney 1982). However, for Lake Tahoe the change in ratio does correspond with a change from ultraoligotrophic to oligotrophic conditions. The stability of diatom community composition at lower depths indicates how unique and dramatic this recent shift in A/C ratio is. While this profile is only 30 cm deep, much longer profiles for the entire Holocene show that diatom and chrysophyte communities have been remarkably stable (Whiting et al. 1989; Carney, unpub. data) in Sierra Nevada lakes. This underscores the utility of diatoms for detecting significant anthropogenic impacts.

Monitoring phytoplankton counts also reveal some interesting changes. During 1969 there is a substantial shift in diatom composition discussed above that includes the decline in *Fragilaria pinnata* and abrupt increases in *Synedra radians* and *Asterionella formosa* (Fig. 1). *Fragilaria crotonensis* and *Melosira italica*, two clear dominants during 1967–71, decline dramatically by the time of the 1982–87 counts. During the 1980s there is a decrease in the absolute and proportional biomass of diatoms and increase in chrysophyte biomass (especially during the summer) associated with the increasing N:P ratio (Hunter et al. 1990). It will be interesting to compare these more recent changes with additional core studies that include the surface sediments.

Conclusions

For Lake Tahoe, diatom dynamics at a given time scale presently appear to be consistent with, and help explain, dynamics at other time scales. Seasonal dynamics underscore the importance of resource-limited growth, interannual variability is largely attributable to the supply of nutrients during spring mixing, and long-term trends reflect the increasing nitrogen loadings and a changing N:P ratio. However, the interactions and coupling between temporal scales need much more quantitative study (Frost et al. 1988; Powell 1989; Magnuson 1990). For Lake Tahoe diatoms interannual variability in particular is poorly understood and needs to be examined in relation to the other information available (Goldman and Jassby 1990). As comparable long-term data sets become available for other freshwater and marine systems it will be most interesting to make comparisons.

Acknowledgements

The long-term Lake Tahoe research has been supported by the Tahoe Regional Planning Agency, National Science Foundation, United States Geological Survey, Environmental Protection Agency, and many other benefactors.

Literature Cited

BRUGAM, R. B. 1979. A re-evaluation of the Araphidineae/Centrales index as an indicator of lake trophic status. Freshw. Biol. 9:451–460.

BYRON, E. R. AND P. ELORANTA. 1984. Recent historical changes in the diatom community of Lake Tahoe, California-Nevada, U. S. A. Verh. Internat. Verein. Limnol. 22:1372–1376.

BYRON, E. R., C. L. FOLT, AND C. R. GOLDMAN. 1984. Copepod and cladoceran success in an oligotrophic lake. J. Plankton Res. 6:45–65.

CARNEY, H. J. 1982. Algal dynamics and trophic interactions in the recent history of Frains Lake, Michigan. Ecology 63:1814–1826.

———. 1987. Field tests of interspecific resource-based competition among phytoplankton. Proc. Nat. Acad. Sci. 84:4148–4150.

CARNEY, H. J., P. J. RICHERSON, C. R. GOLDMAN, AND R .C. RICHARDS. 1988. Seasonal phytoplankton demographic processes and experiments on interspecific competition. Ecology 69:664–678.

CARNEY, H. J. AND C. R. GOLDMAN. 1988. Seasonal phytoplankton r- and K-selection in oligotrophic Lake Tahoe. Verh. Internat. Verein. Limnol. 23:672–676.

CARNEY, H. J. AND J. J. ELSER. 1990. Strength of zooplankton-phytoplankton coupling in relation to lake trophic state. Pp. 615–631 *in* Large Lakes: Ecological Structure and Function, M. M. Tilzer and C. Serruya, eds. Springer-Verlag, Berlin.

ELSER, J. J., H. J. CARNEY, AND C. R. GOLDMAN. 1990. The zooplankton-phytoplankton interface in lakes of contrasting trophic status: an experimental comparison. Hydrobiologia 1990.

FOLT, C. L. AND C. R. GOLDMAN. 1981. Allelopathy between zooplankton: a mechanism for interference competition. Science 213:1133–1135.

FROST, T. M., D. L. DEANGELIS, S. M. BARTELL, D. J. HALL, AND S. H. HURLBERT. 1988. Scale in the design and interpretation of aquatic community research. Pp. 229–258 *in* Complex Interactions in Lake Communities, S. R. Carpenter, ed. Springer-Verlag, New York.

GOLDMAN, C. R. 1974. Eutrophication of Lake Tahoe emphasizing water quality. U. S. Environmental Protection Agency Ecological Research Series (EPA-660/3-74-034). Corvallis, Oregon. 408 pp.

———. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. Limnol. Oceanogr. 33:1321–1333.

GOLDMAN, C. R., A. JASSBY, AND T. POWELL. 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. Limnol. Oceanogr. 34:310–323.

GOLDMAN, C. R. AND A. JASSBY. 1990. Spring mixing depth as a determinant of annual primary production in lakes. Pp. 125–132 *in* Large Lakes: Ecological Structure and Function, M. M. Tilzer and C. Serruya, eds. Springer-Verlag, Berlin.

GUILLARD, R. R. L. 1973. Division rates. Pages 289–311 *in* Handbook of Phycological Methods, J. R. Stein, ed. Cambridge University Press, Cambridge.

HAWORTH, E. 1980. Comparison of continuous phytoplankton records with the diatom stratigraphy in the recent sediments of Blelham Tarn. Limnol. Oceanogr. 25:1093–1103.

HUNTER, D. A., C. R. GOLDMAN, AND E. R. BYRON. 1990. Changes in the phytoplankton community structure Lake Tahoe, California- Nevada. Verh. Internat. Verein. Limnol. 24:505–508.

LIKENS, G. E. 1989. Long-Term Studies in Ecology: approaches and alternatives. Springer-Verlag, New York.

MAGNUSON, J. J. 1990. Long-term ecological research and the invisible present. BioScience 40:495–501.

MELACK, J M., S D. COOPER, R W. HOLMES, J G. SICKMAN, K. KRATZ, P. HOPKINS, H. HARDENBERGH, M. THIEME, AND L. MEEKER. 1987. Chemical and biological survey of lakes and streams located in the Emerald Lake watershed, Sequoia National Park. Final Rept. to the California Air Resources Board, contract No. A3-096-32, Sacramento, California.

PAERL, H. W., R. C. RICHARDS, R. L. LEONARD, AND C. R. GOLDMAN. 1975. Seasonal nitrate cycling as evidence for complete vertical mixing in Lake Tahoe, California-Nevada. Limnol. Oceanogr. 20:1–8.

POWELL, T. M. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. Pp. 157–176 *in* Perspectives In Ecological Theory, J. Roughgarden, R M. May and S A. Levin, eds. Princeton University Press, Princeton.

SCHELSKE, C. L., E. F. STOERMER, G. L. FAHNENSTIEL, AND M. HAIBACH. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aq. Sci. 43:407–415.

SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106:433–471.

STOCKNER, J. G. 1972. Paleolimnology as a means of assessing eutrophication. Verh. Internat. Verein. Theor. Angew. Limnol. 18:1018–1030.

VENRICK, E. L. 1990. Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology 71:1547– 1563.

WHITING, M. C., D. R. WHITEHEAD, R. W. HOLMES, AND S. A. NORTON. 1989. Paleolimnological reconstruction of recent acidity changes in four Sierra Nevada lakes. J. Paleolimnol. 2:285–304.

WILLIAMS, N. J. AND C. R. GOLDMAN. 1975. Succession rates in lake phytoplankton communities. Verh. Internat. Verein. Limnol., 19:808–811.

Relationships Between Salinity and Diatom Flora From Some Australian Saline Lakes

by

P. A. Gell

Department of Geography and Environmental Science,
Monash University, Clayton, 3168, Victoria, Australia

and

F. Gasse

Laboratoire d'Hydrologie et de Géochimie Isotopique,
Université de Paris-Sud, 91405, Orsay, Cedex, France

with 2 figures, 2 tables, and 2 plates

Dedicated to Jean-Charles Fontes

Abstract: This preliminary study of modern Australian diatoms as indicators of water salinity covers 32 saline lakes ranging in conductivity from 1,000–195,000 μScm^{-1}. The species assemblages appear to be clearly influenced by salt concentration and ionic ratios, although several taxa appear to be indifferent to these factors (e.g., *Cocconeis placentula*, *Achnanthes delicatula*, *Nitzschia* sp. aff. *fonticola*, and *N.* sp. aff. *palea* var. *debilis*).

The diversity of species appears to be greatest in lakes of lower salinities (<30,000 μScm^{-1}). Oligosaline waters (1–5,000 μScm^{-1}) support the greatest variety of common species, the most widespread being *Amphora veneta*. Assemblages that include *Eunotia lunaris*, *Achnanthes minutissima*, *Stauroneis pachycephala*, and *Navicula angusta* are associated with the least saline of these lakes. *Anorthoneis excentrica*, *Navicula salinarum*, *N. symmetrica*, and *Gomphonema* spp. are recorded only, or most commonly, in oligosaline waters. *Tabularia* sp. aff. *parva* and *Cymbella pusilla* are most commonly recorded in some mesosaline (5–15,000 μScm^{-1}) and oligosaline waters. *Anomoeoneis sphaerophora* is found to be most abundant in polysaline (15–30,000 μScm^{-1}) lakes. *Navicula elegans* and a large, not yet identified *Nitzschia* are characteristic of the eusaline (30–40,000 μScm^{-1}) and metasaline (40–70,000 μScm^{-1}) waters, although *Rhopalodia* sp. aff. *musculus* dominates in one sample from eusaline waters. *Achnanthes brevipes*, *Berkeleya rutilans*, *Amphora coffaeformis*, and *Nitzschia* sp. aff. *latens* seem to be characteristic of the hypersaline (70,000 μScm^{-1}) lakes, in which *Entomoneis paludosa*, *Navicula* sp. aff. *incertata*, and *Hantzschia* sp. aff. *amphioxys* var. *gracilis* are also not uncommon.

Similarities exist in the assemblages recorded here and those described from saline lakes in Africa and elsewhere.

Introduction

It is now well established that qualitative relationships exist between the composition of diatom communities and the salinity (conductivity) of the water in which they inhabit (Gasse et al. 1983; Fritz and Battarbee 1986; Fritz 1990). Diatoms therefore represent a potentially useful tool for the reconstruction of past salinities in lakes.

Fluctuations in the salt content of a lake through time depend upon: (1) the dilution or concentration of lake salts in response to changes in the precipitation-evaporation balance within the catchment area (a climatic parameter); and (2) the input of salts from sources including the atmosphere, and weathering of salt crusts deposited over the basin during previous arid phases. Alternatively, the seepage of heavy brines through a permeable lake bottom may dampen the effect of climatic changes as in Lake Chad for instance (Roche 1983). The interpretation of diatom-inferred salinity along a stratigraphical profile, once calibrated from the modern diatom flora, therefore represents an interesting approach towards reconstructing paleoenvironments and paleoclimates, but it requires a sound understanding of a basin's hydrology.

Australia is a particularly suitable country for such studies because of the existence of a large number of lakes ranging in salinity from fresh to hypersaline. Previous paleolimnological studies (DeDeckker 1982a, 1988) have already demonstrated the richness of the record in terms of climate-induced changes in lake salinity (Taylor et al. 1990).

There have been few extensive studies undertaken of non-marine diatoms in Australia. Of these, most have centered on river or estuarine systems (e.g., Wood 1964; Brady 1979; John 1983; Thomas 1983; Chessman 1985a, 1985b, 1986; Reed and Newall 1989). In addition, Foged (1978) described the diatom flora from a wide range of aquatic environments in eastern Australia. More recently Holland and Clark (1989) have described the diatom flora of an upland, freshwater reservoir in New South Wales, and Blinn (1991) described that of the saline Lake Eyre in South Australia.

The most extensive treatises of Australian salt lake diatom floras have been by Yezdani (1970) and Tudor (1973). Yezdani focused on some lakes of the Victorian western plains while Tudor examined a wider range of lakes, from fresh to hypersaline, in the states of Victoria, Tasmania, and South Australia. In both studies the influence of a range of environmental factors, including salinity, on the occurrence of diatom taxa was examined and applied to the fossil diatom records of Victorian saline, crater lakes for the purpose of reconstructing their Holocene paleoenvironments. The abundance of the modern diatom species observed by Tudor was estimated using a simple five-category system, and his attempt to establish numerical relations between these flora and the measured aquatic parameters was restricted to the generic level.

A large number of lakes of varying salinity have been sampled in western Victoria to establish relationships between aquatic conditions and taxon abundance, with a view to the development of transfer functions for extrapolation to the past. Although still preliminary, this study of 32 sites from a wide range of biotopes is to date both the most extensive study of the diatom flora of inland saline lakes in Australia and the first attempt to quantify the relationship between Australian diatom species and lake conductivity.

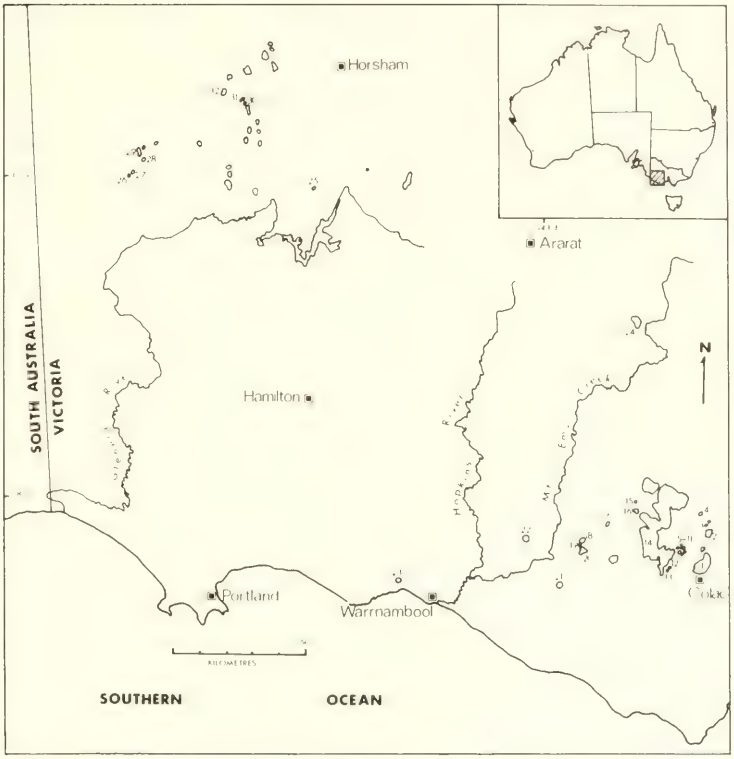


FIGURE 1. Sites of diatom and water sampling (Key to lakes: 1, Lake Colac; 2, Lake Beeac; 3, Lake "WP4"; 5, Red Rock Tarn; 6, Lake Werangunuk; 7, West Twin Lake; 8, Lake Purdigulac; 9, Lake Coragulac; 10, Lake Gnalinegurk; 11, Lake "X"; 12, East Basin; 13, West Basin; 14, Lake Corangamite; 15, Lake Coradgil; 16, Lake Terangpom; 17, Lake Kariah; 18, Lake Gnotuk; 19, Saddle Lake; 20, Lake Bullenmerri; 21, Lake Elingamite; 22, Lake Keilambete; 23, Tower Hill; 24, Lake Goldsmith; 25, Telangatuk East; 26, Immensal Lake; 27, Lake Cogambul; 29, Lake Yallakar; 30, Jacka Lake; 31, "North-west Jacka Lake"; 32, St. Mary's Lake.

Materials and Methods

THE STUDY AREA

All the lakes examined lie within western Victoria, southeastern Australia (Fig. 1). Twenty-four are found in the western basaltic volcanic plains while seven occur in the southern reaches of the Murray-Darling Rivers basin. One site lies in the upper reaches of the Glenelg River basin. Those in the Corangamite region of the western plains (Nos. 1–24) are generally crater or depression lakes in small closed basins as defined by DeDeckker (1982b), although Lake Corangamite, itself 251.6 km^2, could be considered to fall into his category of "large closed basins." None of these are supplied by an extensive drainage

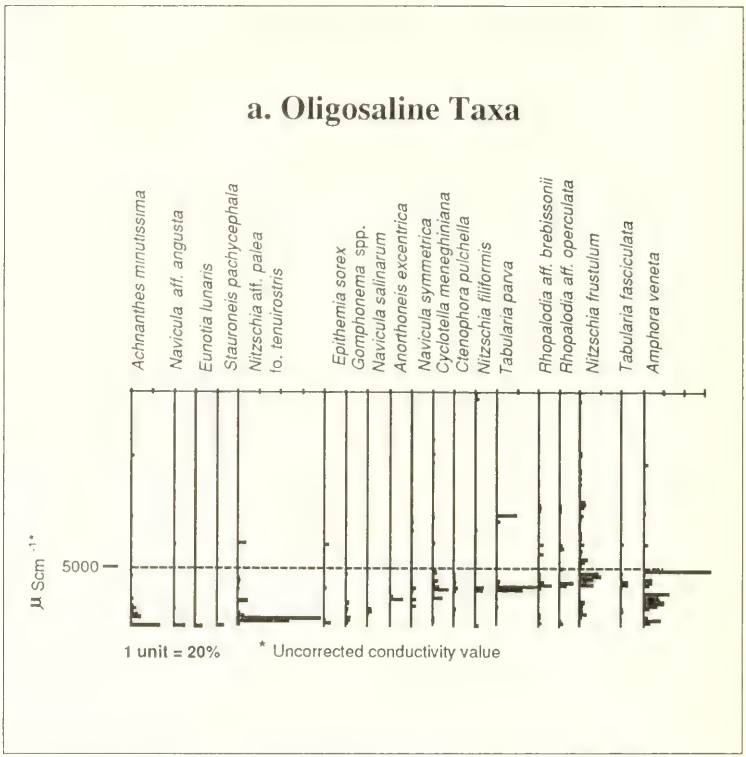


FIGURE 2a. The frequency of selected Oligosaline taxa within conductivity class.

system and some are even isolated from the regional groundwater. The water levels of these lakes in particular closely reflect the precipitation/evaporation ratio. Those to the north (Nos. 25–32) are outside the basaltic plains and were chosen on the basis of their resultant lower carbonate-bicarbonate contents (DeDeckker, pers. comm.). They are also generally in small, closed basins, although the most saline of these could attribute their origin to being sites of groundwater discharge from the large regional aquifer (DeDeckker, pers. comm.).

The study area rests in the temperate climatic zone that receives average annual rainfall of about 500–600 mm (Bayly and Williams 1966). It has a winter wet season. The average summer and winter temperatures for the Corangamite region are 19° C and 8° C respectively (Thomson 1971, cited in DeDeckker and Last 1988). Temperature extremes are greater in the region of the northern group of lakes where summer maximum temperatures above 35° C and winter frosts are not uncommon. Such extremes are relatively rare in the south.

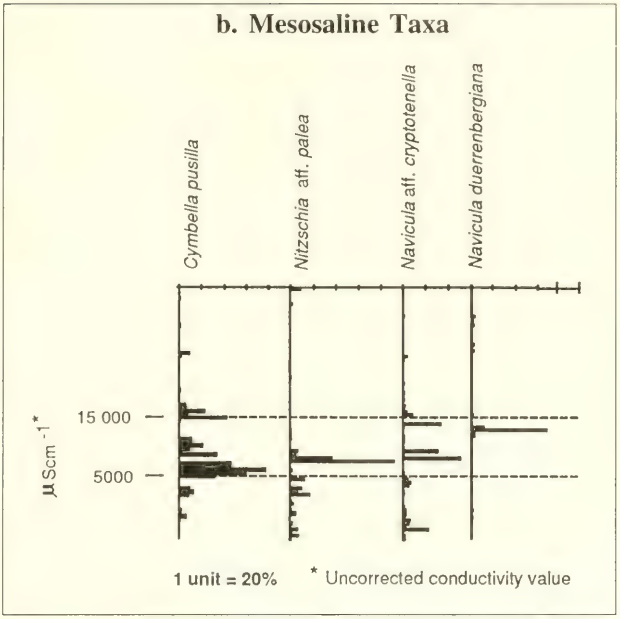


FIGURE 2b. The frequency of selected Mesosaline taxa within conductivity class.

Australian saline lakes are typically dominated by the ions Na^+ and Cl^- (DeDeckker 1983), and the available data on the lakes examined reveal that they are not exceptions (Table 1). Those that lie within the volcanic plains, however, receive solutes weathered and leached from the surrounding rocks as well as the cyclic NaCl salt and so are also variously rich in Mg^{2+}, Ca^{2+}, K^+, SO_42-, HCO_3-, and CO_32- ions (Maddocks 1967; DeDeckker and Williams 1987; DeDeckker pers. comm). The high salinity, pH, and water chemistry of some of these lakes appears to favor the precipitation of carbonates such as dolomite (DeDeckker and Last 1988).

SAMPLE COLLECTION AND PROCESSING

Diatom and water samples as well as pH and conductivity measurements were taken from the selected lakes in November, 1987. All have conductivities greater than 1000 μScm^{-1}, while none of the highly saline lakes have pH values below 8.3.

The conductivity values for high salinity waters were obtained by diluting with distilled water and multiplying the metered result by the dilution factor. As the slope of the relation between conductivity and salinity of solutions decreases with increasing salinity, a correction would be needed. In the case of Na^+Cl^--type waters such as these, this correction would be small. Water chemistry evidence presented here is derived from the literature or DeDeckker (pers. comm.). The planktonic diatom floras were collected using a 60 µm plankton net dragged at the water's surface near the lake edge. The results of 13 such

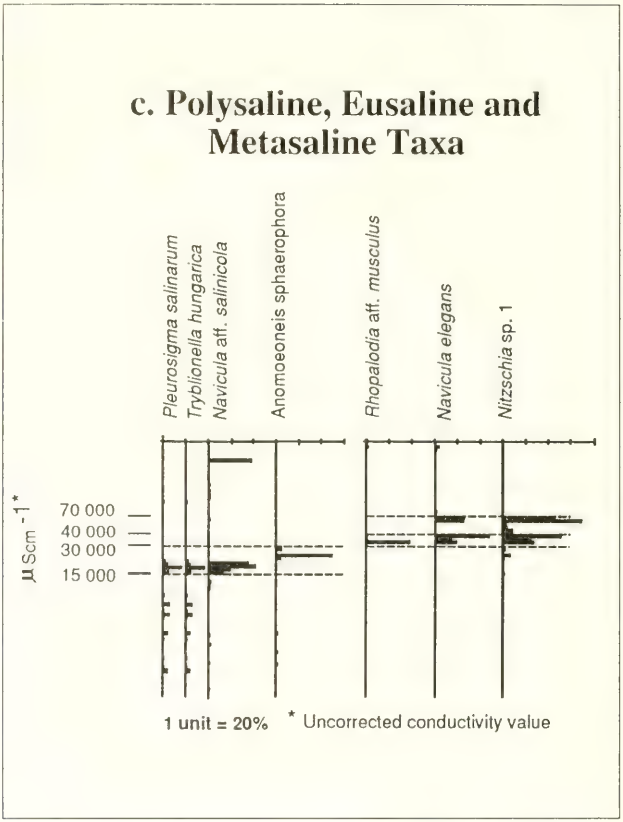


FIGURE 2c. The frequency of selected Polysaline, Eusaline and Metasaline taxa within conductivity class.

samples are presented here. All other samples were taken from scrapings from floating or submerged objects, including macrophytes and other algae.

Some of the lakes under investigation show large seasonal and interannual fluctuations in lake level and salinity. It is therefore preferable, in order to establish accurate relationships between the flora and salinity, to sample living diatoms and measure the ecological variable at the same time. To ensure that the diatoms collected were living at the time of sampling, they were examined for living organelles prior to treatment.

In most cases 600 diatom frustules were counted among four slides from each sample and several samples from a range of habitats were taken from each lake. In some of the less saline lakes only 300 frustules have been counted.

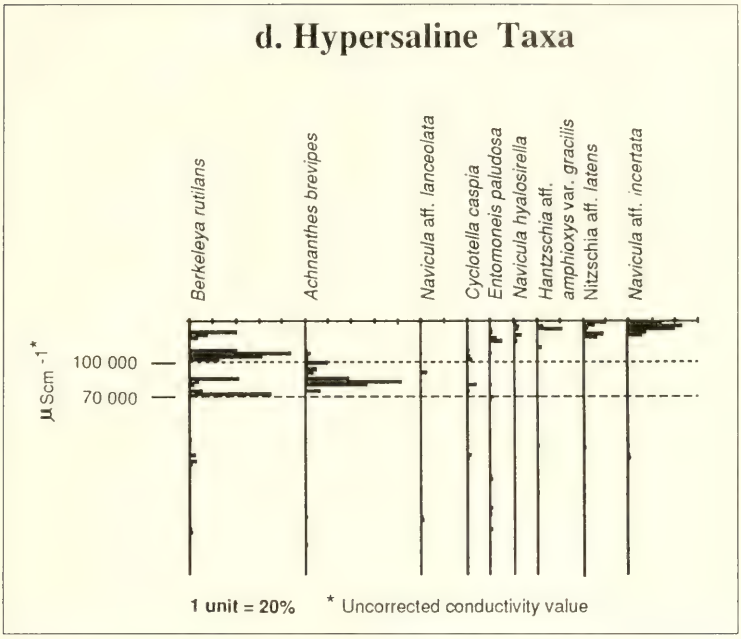


FIGURE 2d. The frequency of selected Hypersaline taxa within conductivity class.

Results and Discussion

The abundance of each of the more commonly encountered species relative to water conductivity is presented in Figures 2a–e. They are placed in categories according to their apparent salinity tolerance following the classification of athalassic waters based on total salinity proposed by Gasse et al. (1987). Each bar represents the relative abundance of the species in a sample, and the samples are ranked according to lake conductivity. Samples from different habitats within the same lake are juxtaposed. As most of the lakes were found to be alkaline at the time of sampling and are known to be NaCl dominant, little quantitative information on pH and chemical composition tolerances can be gained from these results, however, some observations are made.

Several species appear to be salinity indifferent, being found in lakes of a wide range of conductivities. These include *Achnanthes delicatula*, *Cocconeis placentula*, *Nitzschia* sp. aff. *fonticola*, and *N.* sp. aff. *palea* var. *debilis*.

The oligosaline lakes examined generally support the greatest diversity of taxa (Table 1). Several species are present only in the least saline of the oligosaline lakes examined. Their preference for low-salinity waters is supported by additional observations in nearby lakes of conductivities less than 1000 μScm^{-1}. These include *Entomoneis costata*, *Eunotia lunaris*, *Navicula* sp. aff. *angusta*, and *Stauroneis pachycephala*. Other species that are recorded only, or most frequently, in oligosaline waters are *Achnanthes minutissima*, *Am-*

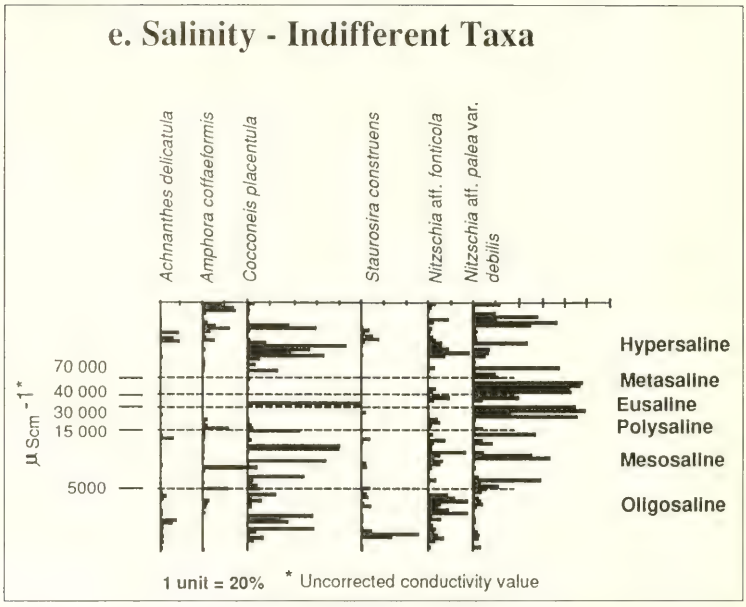


FIGURE 2e. Diatoms species apparently indifferent to conductivity

phora veneta, *Anorthoneis excentrica*, *Epithemia sorex*, *Gomphonema* spp., *Navicula salinarum*, *N. symmetrica*, *Nitzschia* sp. aff. *palea* f. *tenuirostris*, *Rhopalodia* sp. aff. *brebissonii*, *R.* sp. aff. *operculata*, *Ctenophora pulchella*, and *Tabularia fasciculata*. Those species also found in eastern Africa (Gasse 1986) and elsewhere in Australia (Foged 1978; John 1983) generally display similar salinity requirements, although there are some exceptions. *Rhopalodia* sp. aff. *operculata* (and probably *R.* sp. aff. *brebissonii*) is considered to be a species of mostly raised electrolytic content (Krammer 1988), as is most of the *R. gibberula* group. *Navicula salinarum* is considered to be mesohalobous and euryhalabous by Foged (1978), and John (1983) found it to be common in waters that attained salinity levels measuring more than 20 gl^{-1} in the dry season. Additionally, Patrick and Reimer (1966) found *N. salinarum* to occupy brackish waters, or those of a high mineral content in the United States. *Nitzschia hybrida* is considered mesohalobous by Foged (1978). *Nitzschia* sp. aff. *palea* f. *tenuirostris*, a name of uncertain taxonomic status, has been used as it closely resembles the specimens presented under this title by Lange-Bertalot (1980) and Foged (1978).

Although both *Cymbella pusilla* and *Tabularia* sp. aff. *parva* are found commonly in some oligosaline waters, they appear to be more characteristic of the slightly more saline, mesosaline lakes. Additionally, *Navicula* sp. aff. *cryptotenella*, *Nitzschia* sp. aff. *palea*, and a compact form of *Navicula duerrenbergiana* appear to be most common in mesosaline waters, although the first two are also found elsewhere.

Of the two polysaline lakes sampled, one, Red Rock Tarn (pH = 10.0), is characterized by *Anomoeoneis sphaerophora* and the other, Lake Goldsmith (pH = 9.5), by *Navicula* sp. aff. *salinicola*. The shallow, highly alkaline, sodium carbonate-bicarbonate waters of these lakes are very similar to those of alkaline east African lakes such as Lake Abiyata (pH = 9.3–9.5), for example, in which Gasse (1986) also found *Anomoeoneis sphaerophora* in abundance as plankton. It was not recorded in Lake Goldsmith. Interestingly, Red Rock Tarn is one of the most productive lakes in the world, considered to be a consequence of its high, natural orthophosphate content (Hammer 1981). Although Lowe (1974) does not note any nutrient requirement for *A. sphaerophora*, it has been recorded from organically enriched waters (Schoeman 1972; Schoeman and Ashton 1982; Johansen et al. 1983). This result, therefore, may further suggest an association between *A. sphaerophora* and highly productive, P-rich waters. Round and Mann (1981) consider it to be a species of sulphate-rich waters, however, no sulphates were detected in the Red Rock Tarn waters during a recent study (DeDeckker, pers. comm.).

Both metasaline and one of the two eusaline lakes sampled were dominated by a combination of *Navicula elegans* and a yet-to-be identified species of *Nitzschia* (sp. 1) with apparent affinities to the *N. latens* group. Most specimens were between 50 and 90 µm in length and 11 and 15 µm in breadth and with 9–11 fibulae and more than 30 wavy striae in 10 µm (Fig. 3). In one of the samples from the eusaline lake, *Rhopalodia* sp. aff. *musculus* was co-dominant. Krammer (1988) uses < 15 puncta in 10 µm as the key character in separating both *R. musculus* and *R. crassipunctata* from the other species of the *R. gibberula* group. The puncta of these specimens are clear, yet with a density between 12 and 18/10 µm, they have been tentatively separated from the *R.* sp. aff. *brebissonii* recorded in other lakes. The other eusaline lake was found to be almost entirely dominated by *Cocconeis placentula* and varieties, taxa previously recognized as being highly eurysaline (Gasse et al. 1987; Ben Khelifa 1989).

While *Berkeleya rutilans* and *Amphora coffeaeformis* were characteristic of the full range of eusaline waters sampled, *Achnanthes brevipes* and *Cyclotella caspia* showed a preference for waters with conductivities less than 100,000 μScm^{-1}, whereas *Hantzschia* sp. aff. *amphioxys* var. *gracilis*, *Navicula hyalosirella*, *N.* sp. aff. *incertata*, and *Nitzschia* sp. aff. *latens* tolerated the most saline lakes. Most of these observations appear to be consistent with the literature (Hustedt 1961–66; Tudor 1973; Lowe 1974; Foged 1978; John 1983; Gasse 1986; Krammer and Lange-Bertalot 1986; Dor and Ehrlich 1987). However, *Hant-zschia amphioxys* is generally considered as an aerophilous, freshwater form. The specimens encountered in two lakes here are tentatively identified as resembling most closely the drawings of Cleve-Euler (1952). The species is noted in Lowe (1974) as being oligohalobous-indifferent and capable of withstanding osmotic changes by forming inner valves (Cholnoky 1968) as in many aerophilous forms. Additionally, Tudor (1973) records it from his modern samples of western Victoria in waters with salinities as high as 43.0 gl^{-1}. The form recorded here is possibly a saline water variety. *Navicula* sp. aff. *incertata* resembles the description of *N.* sp. aff. *salinicola* from Gasse (1986), which was also found in the most saline of the waters examined. The taxonomy here follows Krammer and Lange-Bertalot (1986), who distinguish the two species on the number of striae and the presence of a central area.

Conclusion

The results from this preliminary study confirm that a clear relationship exists between diatom taxa and the conductivity of the lake waters examined. Evidently, paleosalinity can be inferred from fossil diatom assemblages in the region. Quantitative reconstructions

of paleosalinity require the development of transfer functions. We consider it premature to attempt to develop these from our present data set, since further work is needed to sample the full range of habitat types and seasonal change. In addition, further sampling of lakes is required to attain the equal representation of the conductivity classes necessary for sound statistical results.

Acknowledgements

This work has been funded by the Ministère des Relations Extérieures and the Centre National de la Recherche Scientifique, France. We are grateful to M. Ronis for the development of French-Australian collaborative research programs. We thank P. DeDeckker and M. A. J. Williams for financial arrangements and comment and guidance during field and laboratory work. A. P. Kershaw, G. Clark, and M. A. J. Williams provided funds for P. Gell to attend the conference. P. DeDeckker and J-Ch. Fontes provided comments on the manuscript.

Literature Cited

BAYLY, I. A. E. AND W. D. WILLIAMS. 1966. Chemical and biological studies on some saline lakes of south-east Australia. Australian J. Mar. Freshw. Res. 17:177–228.

BEN KHELIFA, L. 1989. Diatomées continentales et paléomilieux du Sud-Tunisien (PALYHYDAF site 1) au Quaternaire supérieur. Approche statistique basée sur les diatomées et les milieux actuels. Unpublished Ph.D. thesis, Université de Paris XI. 339 pp.

BLINN, D. W. 1991. The diatom flora of Lake Eyre South: a large episodically filled salt lake in South Australia. Hydrobiol. 210:101–104.

BRADY, H. T. 1979. Diatom flora of Australia: Report 1. Freshwater diatoms of the Northern Territory, especially in the Magela Creek system. Macquarie University Press, Sydney. 74 pp.

CHESSMAN, B. C. 1985b. Phytoplankton of the LaTrobe River, Victoria. Australian J. Mar. Freshw. Res. 36:115–122.

———. 1985b. Artificial-substratum periphyton and water quality in the lower La Trobe River, Victoria. Australian J. Mar. Freshw. Res. 36:855–871.

———. 1986. Diatom flora of an Australian river system: spatial patterns and environmental relationships. Freshw. Biol. 16:805–819.

CLEVE-EULER, A. 1952. Die Diatomeen von Schweden und Finnland. K. Svenska VetensAkad. Handl. Fjärde Serien 5:1–153.

CHIVAS, A. R., P. DEDECKKER, AND J. M. G. SHELLEY. 1986. Magnesium content of non-marine ostracod shells: a new palaeosalinometer and palaeothermometer. Palaeogeogr. Palaeoclimat. Palaeoecol. 54:43–61.

CHOLNOKY, B. J. 1968. Die Ökologie der Diatomeen in Binnengewässern. Cramer, Lehre. 699pp.

DEDECKKER, P. 1982a. Holocene ostracods, other invertebrates and fish remains from cores of four maar lakes in southeastern Australia. Proc. R. Soc. Victoria 94:183–220.

———. 1982b. Australian aquatic habitats and biota: their suitability for palaeolimnological investigations. Trans. R. Soc. S. Australia 106:145–153.

———. 1983. Australian salt lakes: their history, chemistry and biota—a review. Hydrobiol. 105:231–244.

———. 1988. An account of the techniques using ostracodes in palaeolimnology in Australia. Palaeogeogr. Palaeoclimat. Palaeoecol. 62:463–475.

DEDECKKER, P. AND W. LAST. 1988. Modern dolomite deposition in continental, saline lakes, western Victoria, Australia. Geology 16:29–32.

DEDECKKER, P. AND W. D. WILLIAMS. 1987. Physico-chemical limnology of eleven, mostly saline permanent lakes in western Victoria, Australia. Hydrobiol. 162:275–286.

DOR, I. AND A. EHRLICH. 1987. The effect of salinity and temperature gradients on the distribution of littoral microalgae in experimental solar ponds, Dead Sea area, Israel. P. S. Z. N. I: Mar. Ecol. 8:193–205.

FOGED, N. 1978. Diatoms in eastern Australia. Bibl. Phycologica 41:1–243.

FRITZ, S. C. 1990. Twentieth-century salinity and water-level fluctuations in Devil's Lake, North Dakota: test of a diatom-based transfer function. Limnol. Oceanogr. 35:1771–1781.

FRITZ, S. C. AND R. W. BATTARBEE. 1986. Sedimentary diatom assemblages in freshwater and saline lakes of the Northern Great Plains, North America: Preliminary results. Pp. 265–271 *in* Proceedings of the 9th International Diatom Symposium, F. E. Round, ed. BioPress Ltd., Koeltz Scientific Books, Bristol, Koenigstein.

GASSE, F. 1986. East African diatoms, taxonomy, ecological distribution. Bibl. Diatomologica 11:1–201.

GASSE, F., J. F. TALLING, AND P. KILHAM. 1983. Diatom assemblages in East Africa: classification, distribution and ecology. Rev. d'Hydrobiol. Trop. O. R. S. T. O. M. 16:3–34.

GASSE, F., J-CH. FONTES, J. C. PLAZIAT, P. CARBONEL, I. KACZMARSKA, P. DEDECKKER, I. SOULIÉ-MARSCHE, Y. CALLOT, AND P. A. DEPEUBLE. 1987. Biological remains, geochemistry and stable isotopes for the reconstruction of environmental and hydrological changes in the Holocene lakes from North Sahara. Palaeogeogr. Palaeoclimat. Palaeoecol. 60:1–46.

HAMMER, U. T. 1981. Primary production in saline lakes. Hydrobiol. 81:47–57.

HOLLAND, J. AND R. L. CLARK. 1989. Diatoms of Burrinjuck Reservoir, New South Wales, Australia. Commonwealth Scientific and Industrial Research Organization, Division of Water Resources, divisional report 89/1. Canberra. 79 pp.

HUSTEDT, F. 1961–1966. Die Kieselalgen Deutschlands, Österreichs und der Schweiz. Teil 7, Pt. 3. *In* Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Part 3, L. Rabenhorst, ed. Akademische Verlagsgesellschaft, Leipzig.
816 pp.

JOHANSEN, J. R., S. R. RUSHFORTH, AND J. D. BROTHERSON. 1983. The algal flora of Navajo National Monument, Arizona, U. S. A. Nova Hedwigia 38:501–553.

JOHN, J. 1983. The diatom flora of the Swan River estuary, Western Australia. Bibl. Phycologica 64:1–358.

KRAMMER, K. 1988. The gibberula-group in the genus *Rhopalodia* O. Müller (Bacillariophyceae). Nova Hedwigia 47:159–205.

KRAMMER, K. AND H. LANGE-BERTALOT. 1986. Bacillariophyceae. Teil 1. Naviculaceae. *In* Süsswasserflora von Mitteleuropa, H. Ettl, J. Gerloff, H. Heynig and D. Mollenhauer, eds. Gustav Fischer, Jena. 876 pp.

LANGE-BERTALOT, H. 1980. New species, combinations and synonyms in the genus *Nitzschia*. Bacillaria 3:41–77.

LOWE, R. L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. U. S. Environmental Protection Agency, Program Element No. 1BA027, Ohio. 334 pp.

MADDOCKS, G. E. 1967. The geochemistry of surface waters of the western district of Victoria. Australian J. Mar. Freshw. Res. 18:35–52.

PATRICK, R. AND C. W. REIMER. 1966. The Diatoms of the United States. Volume 1. Acad. Nat. Sci. Philadelphia, Monograph No. 13. Philadelphia. 688 pp.

REED, J. AND P. NEWALL. 1989. An environmental study of the Plenty River. Rural Water Commission of Victoria, Report No. WQ24. Melbourne. 52 pp.

ROCHE, H. 1983. Traçage naturel, salin et isotopique des eaux du système hydrologique du Lac Tchad. Travaux et documents, 117. O. R. S. T. O. M., Paris. 389 pp.

ROUND, F. E. AND D. G. MANN. 1981. The diatom genus *Brachysira* I. Typification and separation from *Anomoeoneis*. Arch. Protistenk. 124:221–231.

SCHOEMAN, F. R. 1972. Diatoms from sewage works in the Republic of South Africa and South-west Africa. Revista de Biologia 8:57–95.

SCHOEMAN, F. R. AND P. J. ASHTON. 1982. The diatom flora of the Pretoria salt pan, Transvaal, Republic of South Africa. Bacillaria 5:63–99.

TAYLOR, G., F. GASSE, W. WALKER, AND J. MORGAN. 1990. The palaeoecological and palaeoclimatic influence of Miocene freshwater diatomite deposits from southern New South Wales, Australia. Palaeogeogr. Palaeoclimat. Palaeoecol. 77:127–143.

THOMAS, D. P. 1983. A limnological survey of the Alligator Rivers region, Northern territory. Part 1. Diatoms (Bacillariophyceae) of the region. Supervising scientist for the Alligator Rivers region, Research Report 3, AGPS, Canberra. 160 pp.

THOMSON, B. R. 1971. The geology and hydrogeology of the Corangamite region. Unpublished M. S. thesis, Faculty of Science, University of Melbourne. 245 pp.

TUDOR, E. R. 1973. Hydrological interpretations of diatom assemblages in two Victorian western district crater lakes. Unpublished M. S. thesis, Faculty of Science, University of Melbourne. 247 pp.

WILLIAMS, W. D. 1981. The limnology of saline lakes in western Victoria. Hydrobiol. 82:233–259.

WOOD, E. J. F. 1964. Ecological relations of Australian estuarine diatoms. Nova Hedwigia 8:527–548.

YEZDANI, G. H. 1970. A study of the Quaternary vegetation history in the volcanic lakes region of western Victoria. Unpublished Ph.D thesis, Monash University, Melbourne. 608 pp.

TABLE 1. Available data on the lakes examined

Lake	Conductivity μScm^{-1}* (uncorrected)	pH*	Major cations	Major anions	Surface area (ha)	Div[2]	Refs[3]
Hypersaline							
Nth-west Jacka	196000	8.35				0.89	
Cundare	180000	9.0	Na^+	$Cl^-SO_4^{2-}$		0.67	2,8
Beeac	142000	8.75	Na^+	$Cl^-SO_4^{2-}$	607	0.67	1,2,8
Keilambete	116000	9.05	Na^+Mg^{2+}	$Cl^-HCO_3^-$	277	0.37	2,5,6
West Basin	107000	9.35			15.8	0.59	4
Gnotuk	101000	8.8	Na^+Mg^{2+}	Cl^-	208	0.68	2,4,5,6,7
East Basin	92500	9.35	Na^+Mg^{2+}	$Cl^-HCO_3^-$	27.4	0.59	4,6
Corangamite	73700	9.25	Na^+Mg^{2+}	Cl^-	25160	0.80	2,3,4,7,9
Metasaline							
WP 4	58800	9.45				0.51	
Weranganuk	44800	9.9				0.15	
Eusaline							
West Twin	33000	9.7	Na^+K^+	$Cl^-HCO_3^-CO_3^{2-}$		0.66	9
Jacka	32600	10.3				0.01	
Polysaline							
Red Rock Tarn	25000	10.0	Na^+K^+	$Cl^-HCO_3^-CO_3^{2-}$		0.31	3,9
Goldsmith	16800	9.5	Na^+Mg^{2+}	$Cl^- HCO_3^-$		1.08	6
Mesosaline							
Coradgil	12300	10.5	Na^+Mg^{2+}	Cl^-	65	0.44	1
Bullenmerri	12100	10.5	Na^+	Cl^-	488	0.93	2,4,5,7
Kariah	12000	9.0	Na^+Mg^{2+}	$Cl^-CO_3^{2-}$	140	0.70	1,2,7
Purdigulac	12000	9.65	$Na^+Mg^{2+}K^+$	$Cl^-HCO_3^-CO_3^{2-}$		0.5	6,9
Gnalinegurk	10600	10.6				0.44	
Immensal Nth	9250	9.9				1.14	
X	8250	9.1				0.38	
Coragulac	6250	9.7	$Na^+Mg^{2+}K^+$	$Cl^-HCO_3^-CO_3^{2-}$	0.55	3,6,9	
Oligosaline							
Yallakar	4250	8.8				0.98	
Tower Hill	4050	7.75	$Na^+Mg^{2+}K^+$	$Cl^-CO_3^{2-}SO_4^{2-}$		1.26	2
Colac	3400	9.2	$Na^+Mg^{2+}Ca^{2+}$	$Cl^-CO_3^{2-}$	2418	0.92	2,4
Terangpom	3200	9.1				0.81	
Cogambul	3200	7.8				0.73	
St. Mary's	2820	8.8				0.64	
Elingamite	2780	9.3	$Na^+Mg^{2+}Ca^{2+}$	$Cl^-CO_3^{2-}$		1.15	2
Saddle	1650	6.3	$Na^+Ca^{2+}Mg^{2+}K^+$	$Cl^-CO_3^{2-}$	1.13	2	
Immensal	1250	7.9				0.63	
TelangatukEast	1200	5.9				0.94	

* denotes taken at the time of diatom sampling

[1] Ions are considered major here if they represent > 5 % of either all cations or all anions and are presented in order of decreasing concentration.

[2] Shannon-Wiener Diversity Index

[3] Key to references: 1 = Bayly and Williams (1966); 2 = Maddocks (1967); 3 = Hammer (1981); 4 = Williams (1981); 5 = DeDeckker (1982b); 6 = Chivas et al. (1986); 7 = DeDeckker and Williams (1987); 8 = DeDeckker and Last (1988); 9 = DeDeckker (pers. comm.).

TABLE 2. A list of species referred to in the text

Achnanthes brevipes Agardh
Achnanthes delicatula (Kütz.) Grunow
Achnanthes minutissima Kütz.
Amphora coffeaeformis (Ag.) Kütz.
Amphora veneta Kütz.
Anomoeoneis sphaerophora (Ehr.) Pfitzer
Anorthoneis excentrica (Donk.) Grunow
Berkeleya rutilans (Trentepohl) Grunow (= *Amphipleura rutilans*)
Cocconeis placentula Ehrenberg
Ctenophora pulchella (Ralfs ex Kütz.) Williams & Round (= *Synedra pulchella*)
Cyclotella caspia Grunow
Cyclotella meneghiniana Kütz.
Cymbella pusilla Grunow
Entomoneis costata (Hust.) Reimer
Entomoneis paludosa (W. Smith) Reimer
Epithemia sorex Kütz
Eunotia lunaris (Ehrenberg) Grunow
Gomphonema angustatum (Kütz.) Rabenhorst
Gomphonema gracile Ehrenberg
Gomphonema parvulum (Kütz.) Kütz.
Gomphonema truncatum Ehrenberg
Hantzschia amphioxys (Ehrenberg) Grunow
Hantzschia sp. aff. *amphioxys* var. *gracilis* Hustedt
Navicula sp. aff. *angusta* Grunow
Navicula sp. aff. *cryptotenella* Lange-Bertalot
Navicula duerrenbergiana Hustedt
Navicula elegans W. Smith
Navicula hyalosirella Hustedt
Navicula sp. aff. *incertata* Lange-Bertalot
Navicula sp. aff. *lanceolata* (Ag.) Ehrenberg
Navicula salinarum Grunow
Navicula sp. aff. *salinicola* Hustedt
Navicula symmetrica Patrick
Nitzschia sp. aff. *fonticola* Grunow
Nitzschia filiformis (W. Sm.) Van Heurck
Nitzschia sp. aff. *fonticola* Grunow
Nitzschia frustulum (Kütz.) Grunow
Nitzschia hybrida Grunow
Nitzschia sp. aff. *latens* Hustedt
Nitzschia sp. aff. *palea* (Kütz.) Grunow
Nitzschia sp. aff. *palea* var. *debilis* (Kützing) Grunow in Cleve *et* Grunow
Nitzschia sp. aff. *palea* fo. *tenuirostris* Lange-Bertalot
Pleurosigma salinarum Grunow
Rhopalodia sp. aff. *brebissonii* Krammer
Rhopalodia crassipunctata Krammer
Rhopalodia gibberula (Ehr.) O. Müller
Rhopalodia sp. aff. *musculus* (Kütz.) O. Müller
Rhopalodia sp. aff. *operculata* (Ag.) Håkansson
Stauroneis pachycephala Cleve
Staurosira construens (Ehrenberg) Williams & Round (= *Fragilaria construens*)
Tabularia sp. aff. *parva* (Kütz.) Williams & Round (= *Fragilaria fasciculata* var. *parva*)
Tabularia fasciculata (Ag.) Williams & Round (= *Synedra tabulata*)
Tryblionella hungarica (Grun.) Mann (= *Nitzschia hungarica*)

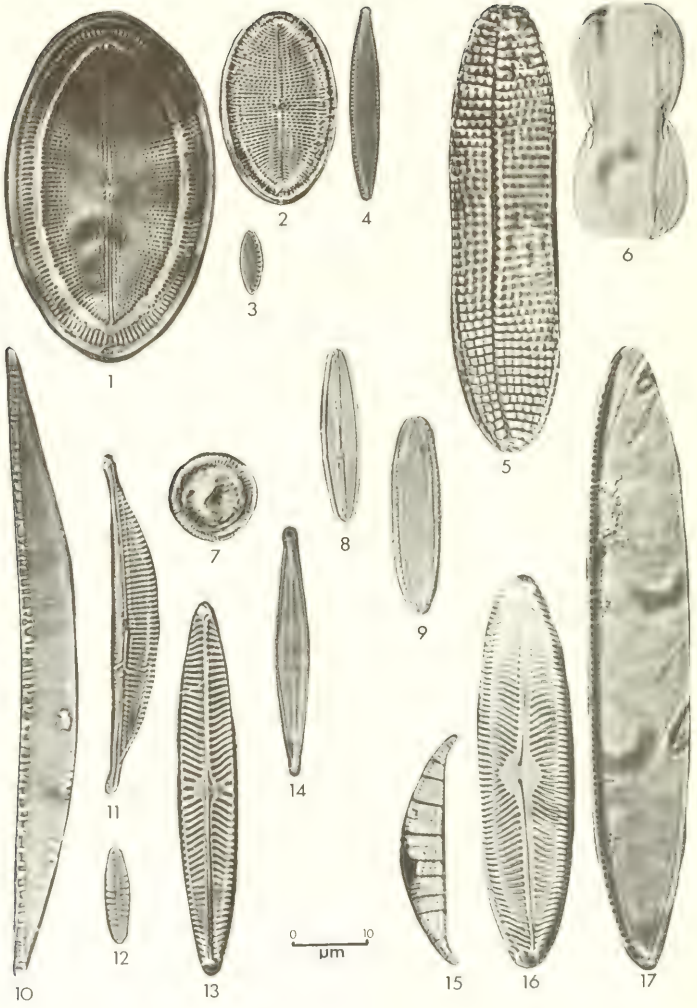
Explanation of Plates

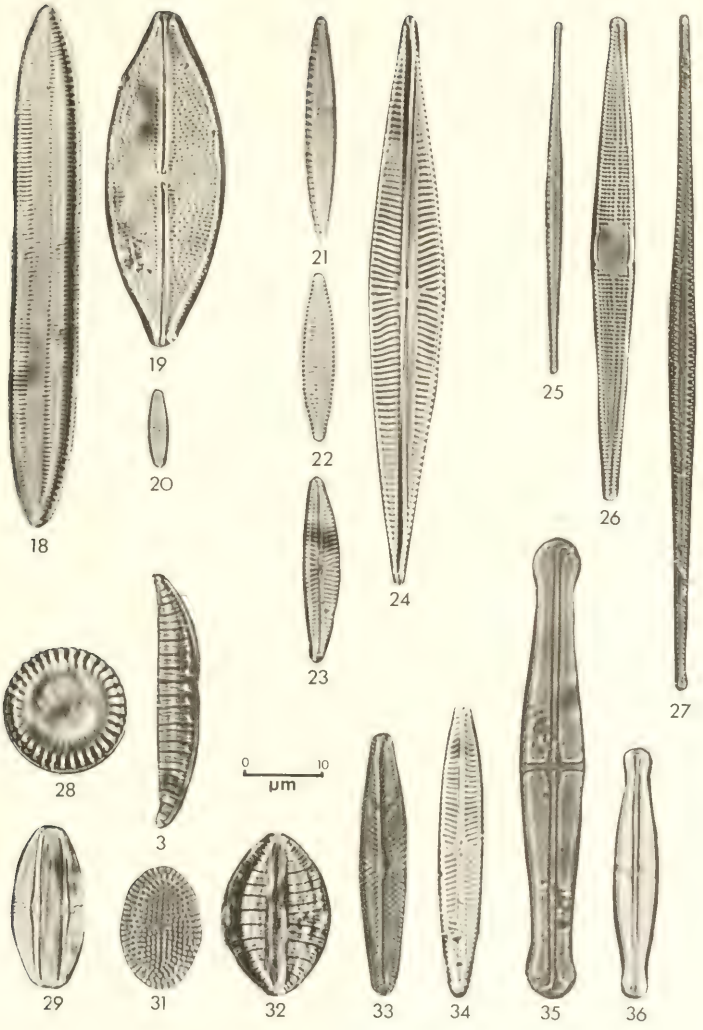
Plate 1, Figures 1–17

FIGURES 1–17. Selected photomicrographs of common taxa from western Victorian saline lakes. FIGURES 1–4. Conductivity indifferent taxa. FIGURES 1, 2. *Cocconeis placentula*. FIGURE 3. *Nitzschia* sp. aff. *fonticola*. FIGURE 4. *Nitzschia* sp. aff. *palea* var. *debilis*. FIGURES 5–14. Hypersaline taxa. FIGURE 5. *Achnanthes brevipes*. FIGURE 6. *Entomoneis paludosa*. FIGURE 7. *Cyclotella caspia*. FIGURE 8. *Berkeleya rutilans*. FIGURE 9. *Nitzschia* sp. aff. *latens*. FIGURE 10. *Hantzschia* sp. aff. *amphioxys* var. *gracilis*. FIGURE 11. *Amphora coffeaeformis*. FIGURE 12. *Navicula* sp. aff. *incertata*. FIGURE 13. *Navicula* sp. aff. *lanceolata*. FIGURE 14. *Navicula hyalosirella*. FIGURES 15–17. Metasaline and Eusaline taxa. FIGURE 15. *Rhopalodia* sp. aff. *musculus*. FIGURE 16. *Navicula elegans*. FIGURE 17. *Nitzschia* sp. 1.

Plate 2, Figures 18–36

FIGURE 18–36. Selected photomicrographs of common taxa from western Victorian saline lakes. FIGURES 18–20. Polysaline taxa. FIGURE 18. *Tryblionella hungarica*. FIGURE 19. *Anomoeoneis sphaerophora*. FIGURE 20. *Navicula* sp. aff. *salinicola*. FIGURES 21–24. Mesosaline taxa. FIGURE 21. *Nitzschia* sp. aff. *palea*. FIGURE 22. *Tabularia* sp. aff. *parva*. FIGURE 23. *Cymbella pusilla*. FIGURE 24. *Cymbella* sp. aff. *pusilla*. FIGURES 25–36. Oligosaline taxa. FIGURE 25. *Nitzschia* sp. aff. *palea* f. *tenuirostris*. FIGURE 26. *Ctenophora pulchella*. FIGURE 27. *Tabularia fasciculata*. FIGURE 28. *Cyclotella meneghiniana*. FIGURE 29. *Amphora veneta*. FIGURE 30. *Rhopalodia* sp. aff. *operculata*. FIGURE 31. *Anorthoneis excentrica*. FIGURE 32. *Rhopalodia* sp. aff. *brebissonii*. FIGURE 33. *Navicula symmetrica*. FIGURE 34. *Navicula* sp. aff. *angusta*. *FIGURES 35, 36. Stauroneis pachycephala*.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
0
10
µm


18
19
20
21
22
23
24
25
26
27
28
3
0
10
µm
29
31
32
33
34
35
36

Diatoms as Indicators of Alkalinity and TOC in Lakes: Estimation of Optima and Tolerances by Weighted Averaging

by

Pertti Huttunen

Karelian Institute, University of Joensuu,
P. O. Box 111, SF-80101 Joensuu, Finland

and

Jaana Turkia

National Board of Waters and the Environment,
Water and Environment Research Office,
P.O. Box 250, SF-00101 Helsinki, Finland

with 1 figure and 1 table

Abstract: Estimated optima and tolerances of alkalinity and total organic carbon (TOC) are presented for diatoms in Finnish lakes. We consider autumnal alkalinity a good measure of lake acidity, and TOC is used to represent the quantity of humic matter in lake water. Surface sediment diatoms were collected from 89 lakes situated largely in southern and central Finland. The study lakes are mostly small and oligotrophic, either acidic or circumneutral, and range from clear to distinctly humic. The alkalinity range of these lakes was from -49 – 405 µeq/L and TOC range from 0.6 – 17.1 mg/L. In estimation of optima and tolerances, the method of weighted averaging was used, assuming that the diatom taxa especially abundant in each lake will be those whose environmental optima coincide with the conditions presented by those lakes.

Introduction

Distributions of diatom taxa are greatly affected by water chemistry and other environmental conditions. As a rule, the species composition of diatom assemblages is closely correlated with pH and with pH-related factors, such as alkalinity. Diatom frustules preserved in lake sediments have proved to be valuable indicators of recent acidification due to acidic precipitation. Historical data on such factors of water quality as pH are generally lacking and when available, they are often insufficient or unreliable for documentation of marked changes in lake water since the beginning of acidic precipitation. However, numerous paleolimnological studies based on diatom stratigraphy have provided

FIGURE 1. Location of the 89 study lakes in Finland.

indirect but clear evidence of recent acidification (e.g., Renberg and Hellberg 1982; Flower and Battarbee 1983; Simola et al. 1985; Tolonen et al. 1986; Huttunen et al. 1990).

In many paleolimnological studies, pH reconstructions have been made by diatom indices (Nygaard 1956; Renberg and Hellberg 1982) based on Hustedt's (1937–39) pH classes for freshwater diatoms. Multiple regression of the pH categories has been an improvement of the inference techniques (see e.g., Charles 1985; Flower 1986). Classification of diatoms into different pH categories may be practical, but it is always more or less subjective. The use of the statistical multiple regression, weighted averaging, and ordination techniques (see e.g., Stevenson et al. 1989; Huttunen and Turkia 1990) involves no such classification, but a calibration dataset of surface sediment diatom assemblages and the corresponding water chemistry is needed. For estimation of indicator values, weighted averaging regression has been used by such diatomists as Berge (1985), Charles (1985), Dixit et al. (1988), and van Dam (1988). The applicability of weighted averaging in calibration has been evaluated by Oksanen et al. (1988), ter Braak and van Dam (1989), and Birks et al. (1990).

Due to regional differences in community composition and in the relationship between diatom assemblages and water quality, local data should preferably be used in all estimations. In this paper, we present optima and tolerances of alkalinity and total organic carbon (TOC) for diatoms in Finnish lakes calculated by weighted averaging regression. We presume alkalinity to be a good measure of lake acidity. It should be at least as reliable as pH. Total organic carbon is widely used in estimating the humic content in natural waters. For that purpose, water color can also be used but it may be less representative because there are other sources of color change, such as high iron concentration.

Materials and Methods

This local dataset of surface sediment diatoms and the corresponding water chemistry includes 89 lakes mainly in southern and central Finland (Fig 1). Most of them are small, oligotrophic, forest lakes with only minor human disturbance in their catchment area. The lakes are either acidic or circumneutral, their pH range being from 4.70 – 7.26 and alkalinity range from - 49 – 405 µeq/L. About 30 % of the lakes are clear water lakes with TOC < 5.0 mg/L, 45 % are humic (TOC 5.0–10.0 mg/L), and nearly 25 % are polyhumic (TOC > 10.0 mg/L).

Most of our study lakes have been part of the biological lake survey of the Finnish Research Project on Acidification. In this project, surface sediment samples were collected in 1985 and 1986 by local water authorities in Finland using gravity corers. Acidic lakes were overrepresented in this material. Therefore, we sampled surface sediments of an additional 20 circumneutral lakes in February, 1988. Five short cores were taken from the deepest basin of each lake. The top 1 cm of sediment was taken with care from the middle of each core, avoiding the core edges. These subsamples were then combined to make one surface sediment sample. Water samples were taken from a depth of 1 m during the 1987 autumnal turnover. Chemical analyses were carried out by the Finnish water authorities using standard methods. Alkalinity has been determined by Gran's method.

Sediment samples were treated with concentrated nitric and sulphuric acids, and cleaned diatoms were mounted in Hyrax. Usually, between 300 and 400 diatom valves were counted in each sample. Sometimes, however, one or two species were so dominant that additional counting was needed. Diatom identification and taxonomy is based mainly on standard floras. However, the taxonomy of the genus *Aulacoseira* is based on Camburn and Kingston (1986) and Haworth (1988). *Navicula cumbriensis*, *N. madumensis*, and *N. subtilissima* were separated according to Haworth et al. (1988). In addition, taxonomy of small *Eunotia* species follows Flower and Kreiser (1988). As a rule, nomenclature and authorities are in accordance with Williams et al. (1988).

Optima and tolerances of alkalinity and TOC for diatoms were estimated by weighted averaging regression. We assume that diatom taxa with certain alkalinity and TOC optima will tend to be most abundant in lakes with alkalinity and TOC values close to these optima. Therefore, an abundance weighted mean of alkalinity or TOC can be regarded as an estimate of a taxon's optimum, u_k:

$$\hat{u}_k = \sum_{i=1}^{n} y_{ik} x_i \Big/ \sum_{i=1}^{n} y_{ik}.$$

A weighted standard deviation is an estimate of a taxon's tolerance, t_k:

$$\hat{t}_k = \left[\sum_{i=1}^{n} y_{ik} (x_i - \hat{u}_k)^2 \Big/ \sum_{i=1}^{n} y_{ik} \right]^{1/2}.$$

Results and Discussion

Studies on the distribution of diatoms in relation to environmental factors have shown that there is often a close correlation between diatom assemblages and pH (e.g., Hustedt 1937–1939; Meriläinen 1967; Charles 1985). Our results confirm that diatom distribution is strongly associated with lake water acidity, which is here quantified by alkalinity (Gran

titration). The abundance of humic matter, here represented by TOC, explains part of the variation of the diatom assemblages but its effect is not as marked as that of acidity. The estimated optima and tolerances of alkalinity and TOC for a selection of diatom taxa are given in Table 1. Taxa occurring with ≥ 1 % abundance in at least one of the 89 lakes were included in estimation (a total of 198 taxa). Originally, the dataset contained more lakes. A few lakes with > 50 % abundance of a single diatom taxon were excluded since overwhelming abundances would prejudice the estimates too heavily.

According to our estimations, *Brachysira serians*, *Eunotia bactriana*, *E. meisteri*, *Navicula tenuicephala*, *N. leptostriata*, *N. hoefleri* sensu Ross & Sims, *N. madumensis*, and *N. cumbriensis* are mostly restricted to acidic, clear-water lakes. Of these species, *N. leptostriata* has the lowest TOC optimum (2.72 mg/L). The distribution of *N. cumbriensis* was a little less limited to clear water lakes but still, this species occurred only in lakes of low alkalinity. Unlike the other above-mentioned diatoms, *N. tenuicephala* has an alkalinity optimum slightly above zero. However, this diatom was abundant in only one lake with measured alkalinity 5 µeq/L and rare elsewhere. Whether clear acidic water is really beneficial to these diatoms and whether the estimated values can be considered true optima remains unresolved. It is more likely that these species are simply acid tolerant and better competitors in the unfavorable environmental conditions.

Asterionella ralfsii is a diatom with a low alkalinity optimum (-10 µeq/L) and a high TOC optimum (11.50 mg/L). We found the species in only six acidic lakes and all of them were more or less humic (TOC 5.7–17.1 mg/L). Other species occurring largely in fairly acidic and humic lakes include *Fragilaria constricta*, *Eunotia serra*, and *E. microcephala*. Thus, the optimal ranges of these *Eunotia* species along the TOC gradient are different from those of *E. bactriana* and *E. meisteri*, occupants of clear acidic water. On the other hand, *E. rhomboidea* was restricted neither to humic nor to clear water lakes. This taxon clearly proved to be indicative of acidic environments with its alkalinity optimum of -23 µeq/L. The estimated optimal alkalinity and TOC values for *E. incisa* (synonym *E. veneris*) are not as reliable because this taxon was abundant in one lake forming 34.5 % of all counted frustules. Otherwise, it occurred in various lakes spanning from acidic to circumneutral and from clear water to humic lakes. As stated by Meriläinen (1967) and Berge (1985), this diatom seems to have a wide amplitude of tolerance to variations in lake water acidity. According to our results, its TOC amplitude is also wide (here from 0.6–17.1 mg/L). *Eunotia incisa* has usually been classified as acidophilous.

Another example of a pair of diatom species with similar alkalinity requirements but a slightly differing distribution in relation to TOC or water color is the acidobiontic *Tabellaria binalis* and *T. quadriseptata*. The estimated alkalinity optima of these taxa are exactly the same (-9 µeq/L). *Tabellaria quadriseptata* seemed to prefer colored waters whereas *T. binalis* was somewhat more often found in clear water lakes, always in low numbers. In contrast, Berge (1985) found both *T. binalis* and *T. quadriseptata* to be characteristic of acidic and humic lakes in Norway.

Semiorbis hemicyclus has often been classified as acidobiontic or acidophilous. In Norwegian material (Berge 1985), this species was a typical inhabitant of acidic lakes, and it had a low weighted pH average (4.7) that corresponds well to the pH optimum (4.76) estimated from the SWAP material by weighted averaging (Birks et al. 1990). In our material, where the maximum relative abundance of *S. hemicyclus* was 6.9 %, this diatom was not as clearly restricted to acidic lakes. Here, the estimated pH optimum is 5.62 and alkalinity optimum 10 µeq/L. This taxon was found both in clear water and humic lakes. The calculated TOC optimum is relatively high (6.39 mg/L). It is evident that differences

in estimated optima of individual diatom species are partly due to dissimilarities between separate calibration datasets.

We studied only a few lakes of circumneutral clear water. In our material, there are not many diatom species with a low TOC optimum and a high alkalinity optimum. Nevertheless, *Achnanthes lanceolata*, *Cyclotella iris*, and *Cymbella cistula* have TOC optima slightly below 5.00 mg/L and alkalinity optima over 200 µeq/L. These species were, however, rarely encountered. Diatom species characteristic of humic or slightly humic circumneutral waters were more numerous. Among these are *Achnanthes didyma*, *A. linearis*, *Asterionella formosa*, *Cyclotella meneghiniana*, *C. stelligera*, *Diatoma tenue* var. *elongatum*, *Navicula rhynchocephala*, and *Synedra ulna*. The calculated optimal TOC and alkalinity values for these species are both comparatively high (Table 1).

Weighted averaging regression is a relatively simple method for estimation of species optima and tolerances. Yet, it has been shown to perform well, for example, when compared with the more sophisticated and computationally more demanding maximum likelihood (see Oksanen et al. 1988; ter Braak and van Dam 1989; Birks et al. 1990). It is obvious that each diatom will grow best only under a particular set of environmental conditions. As with any environmental variable, there are differences between diatom species in respect to alkalinity and TOC requirements; some species are fairly restricted to certain values while others have a wider ecological amplitude. Because of the possible regional differences in diatom responses to environmental variables, a good indicator of alkalinity, for example, in one region may not have similar indicator value elsewhere. At the most, weighted averaging produces only estimates of the true ecological optima, and differences between indicator values point to the need for regional diatom calibration sets.

Acknowledgements

We would like to thank scientists at the Palaeoecology Research Unit, Department of Geography, University College London, especially Roger J. Flower, for help and cooperation in taxonomic updating of the Finnish surface sediment diatom database. The financial support given by the Maj and Tor Nessling Foundation is also gratefully acknowledged.

Literature Cited

BERGE, F. 1985. Relationships of diatom taxa to pH and other environmental factors in Norwegian soft-water lakes. Ph.D. thesis, University of Maine, Orono. 180 pp.

BIRKS, H. J. B., J. M. LINE, S. JUGGINS, A. C. STEVENSON, AND C. J. F. TER BRAAK. 1990. Diatoms and pH reconstruction. Phil. Trans. R. Soc. Lond. Ser. B 327:263–278.

CAMBURN, K. E. AND J. C. KINGSTON. 1986. The genus Melosira from soft-water lakes with special reference to northern Michigan, Wisconsin and Minnesota. Pp. 17–34 *in* Diatoms and Lake Acidity, J. P. Smol, R. W. Battarbee, R. B. Davis, J. Meriläinen, eds. Dr. W. Junk Publishers, Dordrecht.

CHARLES, D. F. 1985. Relationships between surface sediment diatom assemblages and lakewater characteristics in Adirondack lakes. Ecology 66:994–1011.

DIXIT, A. S., S. S. DIXIT, AND R. D. EVANS. 1988. The relationship between sedimentary diatom assemblages and lakewater pH in 35 Quebec lakes, Canada. J. Paleolimnol. 1:23–38.

FLOWER, R. J. 1986. The relationship between surface sediment diatom assemblages and pH in 33 Galloway lakes: Some regression models for reconstructing pH and their application to sediment cores. Hydrobiol. 143:93–103.

FLOWER, R. J. AND R. W. BATTARBEE. 1983. Diatom evidence for recent acidification of two Scottish lochs. Nature 305:130–133.

FLOWER, R. J. AND A. KREISER. 1988. SWAP diatom taxonomy update number one. Palaeoecology Research Unit, Department of Geography, University College London.

HAWORTH E. Y. 1988. Distribution of diatom taxa of the old genus Melosira (now mainly Aulacoseira) in Cumbrian waters. Pp 138–167 *in* Algae and the Aquatic Environment, F. E. Round, ed. Biopress Ltd., Bristol.

HAWORTH E. Y., K. M. ATKINSON, AND P. S. NEWELL. 1988. Distribution of certain diatom taxa in the waterbodies of Cumbria, U. K. Pp. 17–28 *in* Proceedings of the 9th International Diatom Symposium. F. E. Round, ed. Biopress Ltd. and Koeltz Scientific Books, Bristol and Koenigstein.

HUSTEDT, F. 1937–39. Systematische und ökologische Untersuchungen Über die Diatomeen-Flora von Java, Bali und Sumatra nach dem Material der Deutschen limnologischen Sunda Expedition. Arch. Hydrobiol. Suppl. 15:131–177; 187–295; 393–506; 638–790. Suppl. 16:1–155; 274–394.

HUTTUNEN, P. AND J. TURKIA. 1990. Estimation of paleoalkalinity from diatom assemblages by means of CCA. Pp. 443–450 *in* Proceedings of the 10th International Diatom Symposium, H. Simola, ed. Koeltz Scientific Books, Koenigstein.

HUTTUNEN, P., K. KENTTÄMIES, A. LIEHU, M. LIUKKONEN, T. NUOTIO, O. SANDMAN, AND J. TURKIA. 1990. Paleoecological evaluation of the recent acidification of susceptile lakes in Finland. Pp. 1071–1090 *in* Acidification in Finland, P. Kauppi, K. Kenttämies, and P. Anttila, eds. Springer-Verlag.

MERILÄINEN, J. 1967. The diatom flora and the hydrogen-ion concentration of the water. Ann. Bot. Fenn. 4:51–58.

NYGAARD, G. 1956. Ancient and recent flora of diatoms and Chrysophyceae in Lake Grisbo. Folia Limnol. Scandinavica 8:32– 94; 253–262.

OKSANEN, J., E. LÄÄRÄ, P. HUTTUNEN, AND J. MERILÄINEN. 1988. Estimation of pH optima for sediment diatoms by the methods of weighted averaging, least squares and maximum likelihood, and their use for the prediction of lake acidity. J. Paleolimnol. 1:39–49.

RENBERG, I. AND T. HELLBERG. 1982. The pH history of lakes in south-western Sweden, as calculated from the subfossil diatom flora of the sediments. Ambio 11:30–33.

SIMOLA, H., K. KENTTÄMIES, AND O. SANDMAN. 1985. The recent pH- history of some Finnish headwater and seepage lakes, studied by means of diatoms analysis of ^{210}Pb dated sediment cores. Aqua Fenn. 15:245–255.

STEVENSON, A. C., H. J. B. BIRKS, R. J. FLOWER, AND R. W. BATTARBEE. 1989. Diatom-based pH reconstruction of lake acidification using canonical correspondence analysis. Ambio 18:228–233.

TER BRAAK, C. J. F. AND H. VAN DAM. 1989. Inferring pH from diatoms: a comparison of old and new calibration methods. Hydrobiol. 178:209–223.

TOLONEN, K., M. LIUKKONEN, R. HARJULA, AND A. PÄTILÄ. 1986. Acidification of small lakes in Finland by sedimentary diatom and chrysophycean remains. Pp. 169–199 *in* Diatoms and Lake Acidity, J. P. Smol, R. W. Battarbee, R. B. Davis, and J. Meriläinen, eds. Dr. W. Junk Publishers, Dordrecht.

VAN DAM, H. 1988. Acidification of three moorland pools in the Netherlands by acid precipitation and extreme drought periods over seven decades. Freshw. Biol. 20:157–176.

WILLIAMS, D. M., B. HARTLEY, R. ROSS, M. A. R. MUNRO, S. JUGGINS, AND R. W. BATTARBEE. 1988. A coded checklist of British diatoms. Ensis Publishing, London.

TABLE 1. Estimated optima and tolerances of alkalinity and total organic carbon (TOC) for 111 diatom taxa from 89 lakes in Finland.

Taxon	No. of lakes taxon observed	Maximum value (%)	Alkalinity µeq/L Optimum	Alkalinity µeq/L Tolerance	TOC mg/L Optimum	TOC mg/L Tolerance
Achnanthes altaica (Poretzky) A. Cleve-Euler	23	1.2	126	106	7.47	3.78
A. austriaca Hust.	18	2.0	73	95	6.51	2.86
A. didyma Hust.	27	3.8	158	79	8.79	3.80
A. flexella (Kütz.) Brun	11	1.2	184	108	7.04	2.79
A. flexella var. *alpestris* Brun	22	1.7	172	104	7.75	3.12
A. lanceolata (Bréb. ex Kütz.) Grun.	7	4.2	252	45	4.97	1.18
A. laterostrata Hust.	14	5.8	124	64	5.26	1.91
A. linearis (W.Sm.) Grun.	48	5.1	157	89	8.53	3.23
A. minutissima Kütz.	56	27.2	166	96	7.59	3.06
Actinella punctata Lewis	18	1.5	-6	19	5.69	2.49
Amphora ovalis (Kütz.) Kütz.	32	26.5	276	87	6.01	2.48
Asterionella formosa Hassall	43	32.3	144	93	9.69	2.78
A. gracillima (Hantzsch) Heib.	13	17.9	91	91	10.26	2.81
A. ralfsii W. Sm.	6	5.1	-10	36	11.50	5.09
Aulacoseira ambigua (Grun.) Simonsen	41	34.6	233	123	7.39	2.90
A. distans var. *humilis* (A. Cleve-Euler) R. Ross	9	4.2	205	88	6.91	1.68
A. distans var. *nivalis* (W.Sm.) Haworth	22	14.0	8	69	5.65	3.80
A. distans var. *nivaloides* (Camburn)Haworth	7	3.1	29	64	7.23	3.99
A. distans var. *tenella* (Nygaard) R. Ross	29	19.7	53	69	9.93	4.19
A. italica (Ehrenb.) Simonsen	17	3.4	252	87	7.47	3.32
A. lirata (Ehrenb.) R. Ross	54	22.4	29	49	7.95	4.38
A. lirata var. *alpigena* (Grun.) Haworth	14	33.5	26	28	12.85	3.90

TABLE 1, continued.

Taxon	No. of lakes taxon observed	Maximum value (%)	Alkalinity µeq/L Optimum	Alkalinity µeq/L Tolerance	TOC mg/L Optimum	TOC mg/L Tolerance
A. lirata fo. *biseriata* (Grun.) Haworth	14	4.5	38	64	7.48	3.99
A. lirata var. *lacustris* (Grun.) R. Ross	33	6.3	39	79	6.90	4.05
A. perglabra (Østrup) Haworth	43	6.6	16	48	6.57	3.95
A. perglabra var. *floriniae* (Camburn) Haworth	44	6.9	37	74	7.66	4.27
A. subarctica fo. *subborealis* (Nygaard) Haworth	40	48.9	89	77	7.65	3.50
Brachysira brebissonii R. Ross	68	33.2	25	44	6.93	2.91
B. serians (Bréb. ex Kütz.) Round & Mann	22	13.2	-12	18	3.78	2.42
Cyclotella comta (Ehrenb.) Kütz.	32	32.8	232	77	7.71	3.11
C. iris Brun	6	4.7	210	70	4.61	1.64
C. kützingiana Thwaites	14	20.5	103	48	5.40	2.02
C. kützingiana var. *radiosa* Fricke	45	39.6	92	84	6.84	2.98
C. meneghiniana Kütz.	7	1.8	226	61	9.95	2.67
C. stelligera (Cleve & Grun.) Van Heurck	36	43.8	191	99	10.14	2.80
Cymbella amphicephala Naegeli ex Kütz.	33	8.0	12	46	5.51	4.13
C. cistula (Ehrenb. Kirchner	5	1.1	285	62	4.91	1.33
C. cuspidata Kütz.	12	2.0	186	116	5.63	2.82
C. hebridica (Grun. ex Cleve) Cleve	26	3.0	0	35	5.18	3.56
C. lunata W.Sm.	67	6.3	47	70	6.79	3.56
C. microcephala Grun.	32	3.2	153	98	7.37	3.60
C. minuta Hilse ex Rabenh.	49	7.7	79	111	6.70	3.13
C. naviculiformis Auersw. ex Heib.	33	15.0	186	116	7.46	2.83
C. perpusilla A. Cleve	54	4.9	25	46	6.78	3.40
Diatoma tenue var. *elongatum* Lyngb.	6	9.3	317	44	7.24	1.07
Diploneis elliptica (Kütz.) Cleve	7	1.2	275	72	7.66	3.06
D. finnica (Ehrenb.) Cleve	9	1.0	188	101	5.99	2.76
D. marginestriata Hust.	15	1.4	220	90	8.50	4.03
Eunotia bactriana Ehrenb.	11	2.5	-21	15	3.70	2.39
E. curvata (Kütz.) Lagerst	66	8.9	15	69	5.70	3.23

TABLE 1, continued.

Taxon	No. of lakes taxon observed	Maximum value (%)	Alkalinity µeq/L Optimum	Tolerance	TOC mg/L Optimum	Tolerance
E. iatriensis Foged	35	2.1	10	22	6.38	2.76
E. incisa W.Sm. ex Greg.	70	34.5	5	53	6.93	3.67
E. meisteri Hust.	15	1.9	-17	18	3.55	2.81
E. microcephala Krasske ex Hust.	18	8.0	-14	17	6.25	3.65
E. rhomboidea Hust.	7	6.8	-23	12	4.73	2.15
E. serra Ehrenb.	21	1.9	-2	31	7.59	4.87
E. vanheurckii Patr.	15	1.3	6	37	5.29	3.43
Fragilaria brevistriata Grun.	11	2.7	181	95	6.64	3.05
F. constricta Ehrenb.	17	8.6	-3	26	6.94	3.67
F. construens (Ehrenb.) Grun.	52	11.0	143	117	8.54	3.53
F. pinnata Ehrenb.	19	8.9	221	110	7.88	3.37
F. vaucheriae J.B. Petersen	10	2.1	158	104	7.79	2.27
F. virescens var. *exigua* Grun.	58	15.1	58	91	8.15	4.43
Frustulia rhomboides (Ehrenb.) De Toni	65	20.5	5	29	6.83	4.08
F. rhomboides var. *saxonica* (Rabenh.) De Toni	76	38.5	5	42	5.73	4.03
Gomphonema parvulum (Kütz.) Kütz.	5	2.4	208	53	8.41	2.24
G. acuminatum var. *coronatum* (Ehrenb.) W.Sm.	12	1.0	131	107	9.27	2.88
Gyrosigma acuminatum (Kütz.) Rabenh.	17	2.6	264	59	6.87	2.62
Navicula angusta Grun.	18	1.0	50	48	7.05	2.68
N. arvensis Hust.	38	16.7	9	38	7.13	4.59
N. cocconeiformis Greg. ex Greville	30	4.4	62	84	8.08	3.38
N. cryptocephala Kütz.	17	3.8	180	86	8.06	2.39
N. cumbriensis sensu Haworth	10	2.4	-22	12	4.00	2.33
N. hoefleri sensu Ross & Sims	36	12.2	-8	22	3.80	2.82
N. leptostriata Jørgensen	9	3.0	-6	14	2.72	1.62
N. madumensis Jørgensen	16	36.4	-12	16	2.79	1.73
N. mediocris Krasske	57	4.4	26	53	7.06	4.23
N. pupula Kütz.	61	10.1	141	108	7.30	3.45
N. radiosa Kütz.	48	4.8	171	97	7.86	3.43
N. rhynchocephala Kütz.	18	1.7	171	114	9.44	3.08
N. söhrensis Krasske	11	1.2	-10	14	5.47	3.25
N. tenuicephala Hust.	24	26.6	4	21	2.81	2.21

TABLE 1, continued.

Taxon	No. of lakes taxon observed	Maximum value (%)	Alkalinity µeq/L Optimum	Alkalinity µeq/L Tolerance	TOC mg/L Optimum	TOC mg/L Tolerance
Neidium affine (Ehrenb.) Pfitz.	28	2.7	30	53	6.60	3.49
N. affine var. *amphirhynchus* (Ehrenb.) Cleve	50	5.6	22	59	6.41	3.38
N. iridis (Ehrenb.) Cleve	13	1.0	161	109	6.00	2.73
Nitzschia acula Hatzsch ex Cleve & Grun.	34	1.5	90	101	7.88	3.56
N. frustulum (Kütz.) Grun.	16	2.9	79	90	6.93	3.14
N. palea (Kütz.) W.Sm.	22	4.1	101	91	8.44	3.37
Peronia fibula (Bréb. ex Kütz.) R. Ross	39	1.8	22	41	7.04	3.53
Pinnularia abaujensis (Pant.) R. Ross	50	14.3	135	151	6.94	2.93
P. biceps Greg.	77	19.9	32	64	6.13	3.45
P. brauniana (Grun. ex A. Schmidt) Cleve	23	9.0	19	61	6.81	4.06
P. hemiptera (Kütz.) Rabenh.	26	3.3	60	106	7.91	4.56
P. microstauron (Ehrenb.) Cleve	24	1.9	104	129	5.59	4.35
P. nodosa (Ehrenb.) W.Sm.	25	1.6	163	117	7.52	3.27
P. rupestris Hantzsch	33	6.5	3	33	5.54	4.19
Rhopalodia gibba (Ehrenb.) O. Müll.	6	1.0	270	71	6.32	1.73
Semiorbis hemicyclus (Ehrenb.) Patr.	23	6.9	10	23	6.39	3.44
Stauroneis anceps Ehrenb.	49	6.8	68	77	6.73	3.48
S. anceps fo. *gracilis* Rabenh.	68	24.5	98	125	6.88	3.82
S. phoenicenteron (Nitzsch) Ehrenb.	34	2.3	140	128	6.60	2.91
Stenopterobia sigmatella (Greg.) R. Ross	51	4.5	16	41	7.24	3.71
Surirella delicatissima Lewis	44	2.7	12	41	6.51	3.50
S. robusta Ehrenb.	11	1.5	216	83	6.34	2.97
Synedra acus Kütz.	8	2.6	191	68	9.97	3.27
S. parasitica var. *subconstricta* (Grun.) Hust.	15	2.5	255	64	6.11	3.36
S. ulna (Nitzsch) Ehrenb.	10	1.7	255	53	9.65	3.28
Tabellaria binalis (Ehrenb.) Grun.	19	2.1	-9	19	4.84	3.16
T. fenestrata (Lyngb.) Kütz.	39	43.1	97	79	9.52	3.95
T. flocculosa (Roth.) Kütz.	81	9.8	77	102	7.78	3.44
T. quadriseptata Knudson	33	17.1	-9	23	7.32	3.87

Spatial Variation of Diatom Assemblages in Minami-Aizu Moors, Fukushima Prefecture, Japan: The Effect of Pool Size

by

Kazuhiro Katoh

Department of Biology, College of Arts and Sciences,
University of Tokyo, Komaba 3-8-1, Meguro-ku, Tokyo 153, Japan[1]

with 1 figure and 3 tables

Abstract: To observe the relationship between environmental conditions and species composition of diatom assemblages in dystrophic water, field surveys of periphytic diatom assemblages were carried out at four alpine moors in Minami-Aizu Mountain District, Fukushima Prefecture, Japan. In large (> 50 m^2) pools, *Eunotia pectinalis* var. *minor* (Kütz.) Rabh. and *E. tenelloides* H. Kob. et al. were dominant, while in small (< 3 m^2) pools *Frustulia rhomboides* var. *saxonica* (Rabh.) De Toni was dominant. In medium-sized pools either *Eunotia* or *Frustulia* were usually dominant, but *Asterionella ralfsii* W. Sm. and *Tabellaria flocculosa* (Roth) Kütz. were sometimes dominant. On the ground around pools, either *F. rhomboides* var. *saxonica* or *E. exigua* (Bréb.) Rabh. were dominant.

As for water conditions, water temperature was likely to be higher in small pools than in large pools. From this result it is assumed that in small pools water temperature increases easily and environmental conditions may be more unstable than in large pools. Such instability may restrict diatom growth or affect species composition.

Introduction

Studies of diatom assemblages in moors have usually analyzed pH preferences of the species present (e.g., Van Dam et al. 1981). Of course, species composition is influenced not only by pH, but other environmental parameters as well. Van Dam et al. (1981) have shown that the abundance of *Eunotia exigua* (Bréb.) Rabh. increases as the concentration of sulfate increases. Scherer (1988) discusses that local variation in trophic status and some restrictive conditions such as occasional desiccation have some influence on species composition. Katoh (1991) indicates that stability of environmental conditions may affect species composition, based on the observation that the relative abundance of *Frustulia rhomboides* var. *saxonica* (Rabh.) De Toni is much greater in small pools that in large

Present address: Laboratory of Landscape Architecture and Science, Department of Agriculture, University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo 113, Japan

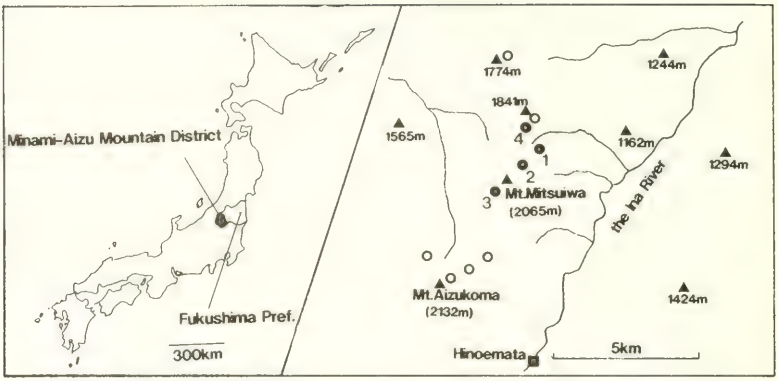


FIGURE 1. Location of study sites. Moors surveyed are numbered 1–4 and indicated by closed circles. Open circles represent other moors. Major peaks are indicated by closed triangles and the altitude given in meters. Rivers and Hinomata Village (closed square) are also shown.

pools although pH does not differ with respect to pool size. The present report evaluates the effect of pool size on species composition of the diatom assemblage from alpine moors in Japan.

Materials and Methods

The Minami-Aizu Mountain District occupies the southwest part of the Fukushima Prefecture of Japan (Fig. 1). Most mountains in the district are 1500–2000 m in height, and some of the mountain tops are nearly flat. These flat areas are where moors are located. Four moors were selected as study sites (Fig. 1).

Field surveys were carried out in June, July, and October 1983, as well as July 1985 and July and October 1989 at 23 pools in the moors. In July 1989, water temperature (WT), pH (by portable pH meter; Horiba Model C-1) and electric conductivity (EC; by portable conductivity meter; TOA Model CM-1K) were measured at some of the pools. Area of all pools was measured roughly and classified into three ranks: large (> 50 m^2), medium, and small (< 3 m^2). All pools were less than 60 cm in depth. Area and depth were positively correlated and, thus, pool size was expressed by pool area.

Diatoms were collected from the surface of dead grasses, living *Sphagnum*, and muddy sediments. Samples were collected from various depths and from the ground around some pools.

Samples were treated as described in Katoh (1991). Cluster analysis (UPGMA) was carried out to classify samples using Bray-Curtis' similarity index (Bray and Curtis 1957).

Results

The relation between water conditions and pool size is shown in Table 1. Because measurements were not carried out on the same day, data analysis and comparisons should be made across samples taken on the same day. No tendency was found in the spatial variation of pH. WT and EC seemed to have a tendency to increase as pool size decreases (Table

TABLE 1. Water conditions and pool size, with average and standard deviation (parenthesized) shown.

date	poolsize	EC	WT	pH	n
7/23	large	8.0 µS/cm	18.0° C	6.1	1
		–	–	–	
	medium	10.1	17.0	6.1	2
		(1.4)	(1.0)	(0.25)	
	small	12.3	18.8	6.3	5
		(1.7)	(1.6)	(0.16)	
7/24	large	11.9	20.5	6.3	2
		(2.7)	(1.6)	(0.15)	
	medium	11.6	19.5	6.2	1
		–	–	–	
	small	16.1	24.1	5.9	3
		(2.7)	(0.33)	(0.25)	

2), though no statistical significance was indicated by the Kruskal-Wallis test (performed as detailed in Sokal and Rohlf 1981). When large and medium pools are united into a single category, a significant difference can be detected between the large + medium pool category and small pools in one case (WT on 24 July) by the Mann-Whitney U test (Sokal and Rohlf 1981).

Samples were classified into six categories, based on cluster analysis. The assemblages of these six clusters, referred to here as Assemblages 1–6, are listed in Table 2. Assemblage 1 was dominated by *Frustulia rhomboides* var. *saxonica* (Table 2). This assemblage was recorded mainly in small pools. Eight samples collected from the ground also were classified in Assemblage 1. Assemblage 2 was dominated by *Asterionella ralfsii* W. Sm. and occurred mainly in medium pools. Assemblage 3 was strongly dominated by *Eunotia pectinalis* var. *minor* (Kütz.) Rabh. and *E. tenelloides* H. Kob. et al. This assemblage was observed in large pools. Assemblage 4 was characterized by having *Tabellaria flocculosa* (Roth) Kütz. as the overwhelming dominant. Dominants in Assemblage 5 included *E. exigua* and *E. fallax* A. Cl., and all samples classified in this assemblage were collected from the ground. Assemblage 6 was dominated by *Eunotia* sp. Assemblage 4 and 6 were found in a total of three samples only and characteristics of these samples were not apparent.

Pool size and habitat appear to be significantly related to the classification of diatom assemblages, while differences in substrate and water depth of habitats did not appear to affect species composition (Table 3). Within- and between-year differences in diatom assemblages were not obvious.

Discussion

Pool size was strongly related to species composition of diatom assemblages. I hypothesize that the stability of environmental conditions influenced the composition of diatom assemblages. Environmental parameters were probably more stable in large pools than in small pools. Diel changes in temperature and weather-related changes in temperature and precipitation probably affect the physical-chemical conditions in small pools more than in large pools. Information about diatom autecologies also suggest environmental variability was negatively related to pool size.

TABLE 2. Relative abundance of major species in the classified assemblages.

taxon	assemblages 1	2	3	4	5	6
F. rhomboides v. *saxonica*	56.6 %	15.3	18.8	9.9	5.5	3.1
F. nipponica	3.2	1.5	0.8	1.2	0.7	0.2
A. ralfsii	5.8	48.9	1.1	7.9	0.1	0.0
E. pectinalis v. *minor*	6.4	13.9	56.3	5.5	12.1	16.5
E. tenelloides	0.6	0.5	9.0	0.0	0.4	0.1
T. flocculosa	2.5	0.1	0.1	65.8	0.0	0.0
E. exigua	7.4	5.9	3.0	2.8	52.7	2 .3
E. fallax	0.8	0.2	0.1	0.2	4.5	0.1
E. sp.	2.7	0.0	3.3	4.0	1.9	73.3

TABLE 3. Assemblages and sampling conditions.

	assemblages 1	2	3	4	5	6
pool size* (except the samples collected from the ground)						
large	0	4	16	0	0	0
medium	14	21	7	3	0	0
small	31	0	1	0	0	3
habitat*						
ground	10	1	0	0	8	0
water	45	25	24	3	0	3
water depth of habitat (in medium or large pools)						
0–10 cm	8	20	15	3	0	0
10–50 cm	6	5	8	0	0	0
substrata						
sphagnum	15	5	3	0	2	0
grasses[1]	33	15	17	3	6	3
mud[2]	7	6	4	0	0	0
season						
spring[3]	1	1	0	0	0	0
summer	38	19	17	3	2	1
autumn	16	6	7	0	6	2
year						
1983	4	3	3	1	0	0
1985	4	2	2	1	0	0
1989	47	21	19	1	8	3

*: sampling conditions and assemblages are not independent ($P < 0.01$)
[1]: dead grasses. [2]: muddy sediment; [3]: late spring, which is the season of thaw (June). Assemblages 4–6 were omitted in the chi-square test. Assemblages 2 and 3 were combined in the test of habitat effect.

Scherer (1988) found that the dominant species of diatom assemblages in a marsh changed with the level of "ecological stress." *Eunotia exigua*, *Frustulia rhomboides* var. *saxonica*, and *Asterionella ralfsii* correspond to quite severe, moderately severe, and less severe "ecological stress," respectively. In the present study *E. exigua* dominated assemblages on the ground. Van Dam (1988) reported that *E. exigua* became dominant in moorland pools after desiccation and suggested the rapid increase in acidity was the reason. Such increases of acidity are caused by the exposure and oxidization of reduced sulphur and nitrogen compounds (Van Dam et al. 1988; Van Dam 1981). Scherer (1988) also suggested that *E. exigua* can survive extreme conditions within an acidic environment.

Frustulia rhomboides var. *saxonica* was dominant in Assemblage 1 and found mainly in small pools. It is assumed that the environment of small pools is unstable and moderately severe for diatoms. Both *E. pectinalis* and *A. ralfsii* are dominant (Assemblages 3 or 2) in the most stable environment, that being large pools. Thus, based on the data at hand, the composition of diatom assemblages in alpine moors in the Minami-Aizu Mountain District may be related to variability in habitat types, from relatively unstable, exposed collections from the ground to the more stable habitat of relatively large pool size.

Acknowledgements

I would like to express my thanks to Dr. H. Kobayasi, president of the Japanese Society of Diatomology and Dr. S. Mayama, Tokyo Gakugei University, for advice on the identification of diatoms.

Literature Cited

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Katoh, K. 1991. Diatom assemblages in a high moor: an observed correlation between species composition and pool size. Jap. J. Phycol. 39:363–368.

Scherer, R. P. 1988. Freshwater diatom assemblages and ecology/palaeoecology of the Okefenokee Swamp/Marsh complex, southern Georgia, U. S. A. Diatom Res. 3:129–157.

Sokal, R. R. and F. J. Rholf. 1981. Biometry. Second Edition. Freeman, San Francisco.

Van Dam, H. 1988. Acidification of three moorland pools in the Netherlands by acid precipitation and extreme drought periods over seven decades. Freshw. Biol. 20:157–176.

Van Dam, H., G. Suurmond and C. J. F. Ter Braak. 1981. Impact of acidification on diatoms and chemistry of Dutch moorland pools. Hydrobiologia 83:425–459.

Estimation of the Recovery of Water Quality in an Urban Water System By the Diatom Flora

by

Sakiko Yoshitake

Shonan Junior College, Yokosuka-shi Kanagawa, Japan

and

Hiroshi Fukushima

Tokyo Women's College of Physical Education,
Kunitachi-shi, Tokyo, Japan

with 1 figure and 4 tables

Abstract: Diatom assemblages of the Iwato River, a stream running through an urban section of central Japan, were investigated to assess changes in water quality. Eutrophication resulted from development of housing around the river, and samples were taken before (June, August, and December 1985) and after (April 1990) construction of a sewerage system.

Dominant attached diatoms in the 1985 samples were *Navicula seminulum*, *Gomphonema angustatum*, and *N. gregaria*, species considered tolerant of water pollution. In the April 1990 samples the dominant species was *Achnanthes lanceolata*, a species comparatively intolerant of water pollution. Increases in species richness and DAIpo values, as well as changes in the dominant species, between 1985 and 1990 suggest recovery of water quality after implementation of the sewerage system.

Introduction

The Iwato River flows through an urbanized section of the Miura Peninsula of central Japan. Water quality of this stream declined due to development of housing nearby. In 1985 domestic sewage flowed into the stream, but by 1990 a sewerage system was implemented in the area. The present report compares changes in water pollution in the Iwato River as estimated by diatom assemblages before and after construction of the sewerage system.

TABLE 1. Relative frequencies of main donimant species in the Iwato River.

Date	Sampling station	Name of species	Relative frequency
'85 June	St. A	*Navicula seminulum*	60
		N. viridula v. *rostellata*	15
		Gomphonema angustatum	14
	St. B	*N. seminulum*	87
	St. C	*G. angustatum*	46
		N. viridula v. *rostellata*	15
		N. seminulum	13
		N. gregaria	10
'85 Aug.	St. A	*G. angustatum*	41
		N. gregaria	23
		N. seminulum	21
	St. B	*G. angustatum*	48
		N. gregaria	23
		N. seminulum	10
	St. C	*G. angustatum*	32
		N. gregaria	30
		N. seminiulum	26
'85 Dec.	St. A.	*G. angustatum*	73
		N. seminulum	13
	St. B	*G. angustatum*	55
		G. subaugur	28
	St. C	*G. angustatum*	68
		N. seminulum	16
'90 Apr.	St. A	*G. angustatum*	15
		N. margalithii	13
		N. menisculus	12
		N. gregaria	11
		Achnanthes lanceolata	10
	St. B	*A. lanceolata*	54
		N. gregaria	13
		N. menisculus	9
		N. viridula v. *rostellata*	8
	St. C	*A. lanceolata*	34
		N. margalithii	23
		G. angustatum	9

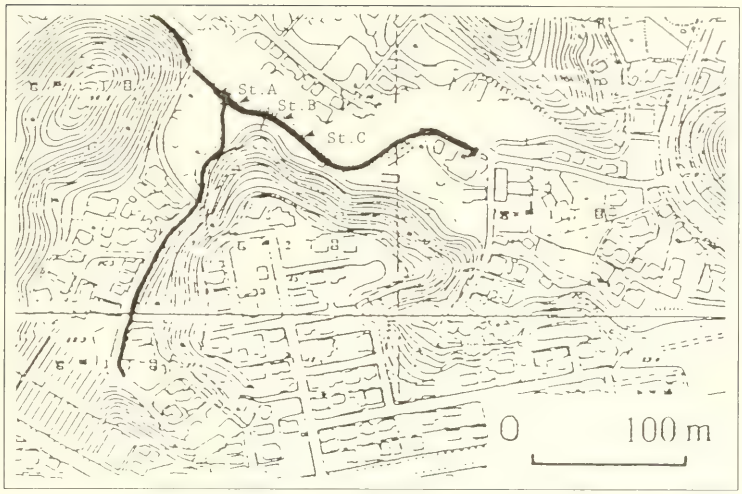


FIGURE 1. Samples were collected at three stations: A, B, and C. The source of this stream is springs about 200 m upstream from the sampling stations.

Materials and Methods

Attached diatoms were sampled from substrates at three stations in June, August, and December of 1985 and in April 1990. Relative frequencies of each diatom taxon and dominant taxa were noted. DAIpo (Diatom Assemblage Index to organic water pollution, see Watanabe 1981) values were calculated as an estimate of water quality relative to organic pollution.

The source of the Iwato River is approximately 200 m upstream from the sites where samples were taken. Volume of springs was almost constant before and after implementation of the sewerage system (Ooba 1989). Differences in maximum and minimum water temperature was 4.5° C, due to the proximity of the springs. The pH of the water was 8.1 for all samples.

Results

DOMINANT SPECIES

As indicated in Table 1, the dominant species appearing in the June, August, and December 1985, samples were *Gomphonema angustatum* (Kützing) Rabenhorst, *Navicula seminulum* Grunow, and *N. gregaria* Donk. In April 1990 samples, the main dominant species were *Achnanthes lanceolata* (Bréb.) Grunow, *G. angustatum* (Kützing) Rabenhorst, *N. margalithii* Lange-Bertalot, and *N. menisculus* Schumann.

SIMILARITY OF DIATOM ASSEMBLAGES BETWEEN DIFFERENT SAMPLING TIMES

The similarity index (Cλ) of Morishita (1959) was used to compare the composition between two assemblages. As Table 2 shows, similarity was low between each station in

TABLE 2. C λ values between sampling times.

Station		'85 Aug.	Dec.	'90 Apr.
A	'85 June	0.6	0.4	0.1
	Aug.		0.8	0.5
	Dec.			0.4
B	'85 June	0.2	0.2	0.0
	Aug.		0.8	0.1
	Dec.			0.0
C	'85 June	0.8	0.9	0.3
	Aug		0.7	0.2
	Dec.			0.2

TABLE 3. Change of number of diatom taxa.

Station	'85 June	Aug.	Dec.	'90 Apr.
A	8	8	7	18
B	7	9	5	19
C	9	9	6	20

TABLE 4. Index, DAIpo values.

Station	'85 June	Aug.	Dec.	'90 Apr.
A	19	39	44	51
B	6	43	45	50
C	42	36	42	52

the April 1990 collections. Low similarity was also found between assemblages at station B in the June 1985 samples, due to the marked domination of *Navicula seminulum*.

Species Richness

The number of taxa in the 1985 samples was relatively small, ranging from 5–9 at the three stations, while the number of taxa recognized in the 1990 samples nearly doubled (Table 3).

Estimation of Organic Water Pollution by the DAIpo Index

Values of the DAIpo index range from 0–100, with larger values indicating weaker organic pollution (= better water quality). Watanabe et al. (1988) reported that DAIpo was a common boundary that distinguished between oligosaprobic and mesosaprobic levels. DAIpo values for the April 1990 samples were larger (≥ 50) than values from the 1985 samples (6–45; see Table 4).

Discussion

The most widely distributed, dominant taxon in the 1985 samples was *Gomphonema angustatum*. Although this species has been described as an oligosaprobic taxon (Hustedt 1957; Fukushima 1969; Sládecek 1973) and a species sensitive to water pollution (Lange-Bertalot 1979; Descy 1979), Watanabe et al. (1986) reported *G. angustatum* to be tolerant of water pollution and distributed over a wide range of trophic types. Consequently, we

conclude this taxon is zenosaprobic to polysaprobic, corresponding to a range of DAIpo values of 0–100.

The second-most dominant species in the 1985 samples was *Navicula seminulum*. It has been reported to be particularly tolerant of pollution (Lange-Bertalot 1979), but also slightly sensitive (Germain 1981). According to Watanabe et al. (1986), this taxon is distributed in zenosaprobic to polysaprobic waters and is abundant in mesosaprobic and, especially, polysaprobic conditions.

Another abundant species in the 1985 samples was *N. gregaria*. Hustedt (1957), Schoeman (1973), Lange-Bertalot (1979), and Germain (1981) described this taxon as being sensitive to water pollution, and Sládecek (1973) considered it a β-mesosaprobic species. Fukushima et al. (1976) found this taxon growing in waters with BOD values of 1–46 ppm and abundantly in waters with BOD values of 1–5 ppm. On the other hand, this taxon is distributed in saprobic to polysaprobic waters and frequently appeared in oligosaprobic to mesosaprobic waters (Watanabe et al. 1986). This taxon can be characterized as a tolerant species.

Achnanthes lanceolata was widely distributed in the 1990 samples. This taxon was described as an oligosaprobe (Hustedt 1957), zenosaprobe to β-mesosaprobe (Sládecek 1973), and a species tolerant of water pollution (Lange-Bertalot 1979). Watanabe et al. (1986) characterized *A. lanceolata* as a zenosaprobic to polysaprobic species, especially an oligosaprobe. Fukushima et al. (1976) found this taxon growing in water with BOD values of 1–4 ppm. In the samples from the River Yagawa (Tokyo), which also has springs as its source and is similar environmentally to the Iwato River, the most widely distributed, dominant species through all seasons was *A. lanceolata* (unpublished data).

Based on the increase in species, larger DAIpo values, and autecologies relative to water pollution of the dominant species in both the 1985 and 1990 samples, water quality of the Iwato River appears to have recovered after implementation of the sewerage system.

Literature Cited

DESCY, J. P. 1979. A new approach to water quality estimation using diatoms. Nova Hedwigia, Beih. 64:305–323.

FUKUSHIMA, H. 1969. Notes on biological water analysis. Bull. Yokohama City Univ. Nat. Sci. 20:33–92.

———. 1976. Relations between algal communities and water quality, especialy BOD and COD1. Jap. J. Water Treat. Biol. 12:16–21.

GERMAIN, H. 1981. Flore des Diatomées eaux douces et saumâtres. Boubée, Paris. 444 pp.

HUSTEDT, F. 1957. Die Diatomeenflora des Flusystems der Weser im Gebiet der Hansestadt Bremen. Abh. naturw. Ver. Bremen. 34:181–440.

LANGE-BERTALOT, H. 1979. Pollution tolerance of diatoms as a criterion for water quality estimation. Nova Hedwigia, Beih. 64:285–304.

MORISHITA, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ., Ser. E. (Biol.). 3:65–79.

OOBA, N. 1989. Recovery of the urban water system, Iwato river, Yokosuka, Kanagawa Prefecture. Sci. Rept. Yokosuka City Mus. 37:9–28.

SCHOEMAN, F. R. 1973. A systematical and ecological study of the diatom flora of Lesotho with special reference to the water quality. V & R Printers, Pretoria. 355 pp.

SLÁDECEK, V. 1973. System of water quality from the biological point of view. Arch. Hydrobiol., Beih. Ergebn. Limnol. 7:1–218.

WATANABE, T. 1981. A new approach to water quality estimation using the specific composition of the benthic diatoms in epilithic forms based on the discussion of several problems on indicator organisms. Environ. Poll. Control 17:13–18.

WATANABE, T., K. NEGORO, H. FUKUSHIMA, H. KOBAYASI, K. ASAI, T. GOTOH, T. NAGUMO, T. KOBAYASHI, S. MAYAMA, AND A. HOUKI. 1986. Studies on the quantitative water quality estimation on freshwater pollution using diatom communities as the biological indicator. Res. Proj. Rev. 1986, Nissan Sci. Found. 139–167.

WATANABE, T., K. ASAI, AND A. HOUKI. 1988. Biological information closely related to the numerical index DAIpo (Diatom Assemblage Index using organic water pollution). Diatom 4:49–58.

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 01302 6018